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Influence of Light and Temperature on the Reproductive Cycle of the Eastern Brook Trout, *Salvelinus fontinalis* (Mitchill)[1,2]

By Nancy E. Henderson[3]

ABSTRACT

Brook trout were exposed to photoperiods ranging from 4 to 20 hours per day and were held either at 8.5°C or at 16°. The average diameter of the ova was used as an index of ovarian development while testicular maturation was determined from histological preparations.

The gonadal cycles of both male and female trout were markedly affected by different photoperiodic regimes. The influence of long or short photoperiods depends upon the phase of gametogenesis in progress at the time and on the photoperiod in effect during earlier stages of the gonadal cycle. Evidence is presented which suggests that the maturation cycle of the gonads may be regulated by the normal seasonal changes of day length.

An accelerated light regime can hasten the time of functional maturity in adult trout, but is without effect when applied to maturing fish in which gametogenesis is taking place for the first time. It is suggested that a stimulative effect of environmental factors is dependent upon maturation of the hypothalamic-hypophyseal mechanism.

The rate of gonadal development is the same at 16° as it is at 8.5° provided the fish are exposed to natural day lengths. If fish are subjected to long or to short photoperiods, the gonadal response at 16° is quite different from that at 8.5°.

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[2]Contribution from the Ontario Fisheries Research Laboratory, which is operated jointly by the University of Toronto and the Ontario Department of Lands and Forests. This paper is taken from a section of a doctoral thesis submitted to the University of Toronto. The data from all experiments are contained in an appendix deposited with the University of Toronto.

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INTRODUCTION

A NUMBER of investigations have been concerned with the role of environmental factors in the regulation of the reproductive cycles of fish inhabiting the temperate regions. Experimental work has been confined to a dozen or so species representing six families, the Salmonidae, Cyprinidae, Cyprinodontidae, Poeciliidae, Gasterosteoidae and Centrarchidae. A brief survey of the findings is precluded because the experimental conditions which have been employed are so diverse, and the results so contradictory, that each investigation would have to be presented with lengthy qualifications. Suffice it to say, that in some species, the length of the photoperiod seems to be the chief regulatory factor, while in others, temperature appears to be more influential. The literature has been critically reviewed by Atz (1957) and more recently by Harrington (1959a) — however, the latter publication is somewhat limited in scope.

Atz (1957) points out that most of the experimental work was too poorly controlled and of too brief duration to allow proper assessment of the roles of light and temperature. He emphasizes the need for lengthy experiments, covering all phases of the reproductive cycle.

For one species at least, the eastern brook trout (*Salvelinus fontinalis*), there has been general agreement among several investigators (Hoover and Hubbard, 1937; Hazard and Eddy, 1951; Corson, 1955). It has been found that if fish are exposed to an accelerated light regime of increasing and decreasing photoperiods, functional maturity can be induced several months in advance of the normal time. (Functional or gonadal maturity refers to the stage in the reproductive cycle in which eggs or sperm can be stripped from the fish.) These results are well established, and this technique has been applied on a commercial scale in several areas of the United States. However, the investigators were concerned only with the time of functional maturity, and no enquiry has been made into the manner in which these effects were achieved. Although the results are of practical value, they merely indicate a photoperiodic effect, and do not provide any information with regard to the roles of different day lengths in the reproductive cycle.

The brook trout normally spawns in late August or in September in the northernmost part of its range (60° N), and during November in the southernmost areas (35° N). At the latitude of Toronto (44° N), spawning occurs in mid October. There the males usually become functionally mature during the first week in October and the females one or two weeks later. For purposes of comparison, the normal time of reproduction, at the latitude of Toronto, is taken to be October 15 throughout this text.

The brook trout normally inhabits streams and rivers, but occasionally is found in the more shallow areas of cold lakes. This distribution clearly indicates that they are subject to the natural fluctuations of day length.

The aim of the present study was to determine the effects of different regimes of light and temperature on the gonadal development of brook trout, with the hope of evaluating the influence of these factors in the regulation of its reproductive cycle.

In the series of experiments to be described, the artificial photoperiods ranged from 4 to 20 hours of light per day. Only two levels of temperature were used, 8.5 and 16° C. These temperatures represent the approximate extremes of the range to which the fish are normally exposed during a major part of the growing season. Hayes (1946) reported that brook trout occurred between the 7 and 21° isotherms in two Nova Scotia lakes and Baldwin (1948) has shown that a population in Redrock Lake, Ontario, is distributed between the 12 and 20° isotherms during the period of thermal stratification in July and August. There are numerous field observations which indicate that brook trout do not usually occur in streams and lakes at points where the water temperature is much above 20° (e.g. Ricker, 1934; Hoover *et al.*, 1937, 1938; Cooper, 1939a, b).

Initial experiments were designed to test the possibility that the time of gonadal maturity could be predicted on the basis of a summation effect of the photoperiodic and thermal experience. This approach was suggested by Burger's (1939a) hypothesis of an additive effect of day lengths in connection with avian reproduction, a concept which was later supported by evidence obtained by Wolfson (1952). Subsequent experiments were designed to determine the effect of different photoperiodic and thermal conditions on the various phases of gonadal maturation. In addition, several different age groups of maturing and adult fish were subjected to an accelerated version of the normal light cycle.

In work of this kind, it is impossible to have control experiments in the commonly accepted definition of this term. However, some standard must be established for comparative purposes. In the present work, fish maintained at 8.5±1° C under natural day lengths at Toronto are referred to as the control group and their gonadal cycle is accepted as representing standard or normal development.

MATERIAL AND METHODS

General Maintenance of Fish

The brook trout were supplied from hatchery stocks maintained by the Ontario Department of Lands and Forests. When fish for each year's series of experiments were delivered to the Maple Laboratory in August or September, they were placed in outdoor holding tanks for a period of approximately 6 months. During this time, the fish were exposed to natural illumination and held at 8.5 ±1°, the temperature of the laboratory water supply. Fish were transferred to the experimental tanks 1 week before the experiments were begun. These tanks were also located out of doors and one tank was allotted to each experiment.

In the initial series of experiments (1957, numbers 1–6), the trout were housed in small rectangular cement tanks, each measuring 6 × 2 × 1.7 feet (183 × 61 × 52 cm) so giving a volume of 600 litres, and each provided with a water flow of 4 litres per minute. Five of the 6 tanks were covered with peaked wooden tops and were accessible through a door at one end of the covers. Light fixtures were mounted in the center of the top of each tank. Two of these tanks were illuminated by two 40-watt Sylvania fluorescent tubes, while the remaining 3 tanks were each equipped with a single 200-watt Sylvania daylight bulb. The intensity of artificial light at the water surface in each tank varied from 8 to 62

foot-candles. The sixth or control tank was covered with wire screening and exposed to natural solar illumination. In 4 tanks, the temperature of the water was held at 8.5±1° throughout the experimental period; in the other 2 tanks it was increased to 16° for part of the experimental period. Hot water was drawn from a steam heated water line and mixed with cold in a Y tube. Rates of flow in the hot and cold lines were adjusted to obtain water of the required temperature which was admitted into the tank. Air diffusers in these fish tanks served to reduce the gaseous content of the water to air equilibrium values.

Six larger wooden tanks were made available for the later series of experiments (1958, No. 6–12; and 1959, No. 13–16). These measured 7.6 × 4 × 1.3 feet (232 × 122 × 40 cm) and had a water volume of 1100 litres. The water flow in these tanks varied between 6 and 7 litres per minute. Each tank was covered with a peaked wooden top, one side of which consisted of 3 hinged lids. In experiments utilizing natural daylight, these lids were replaced by wire mesh screens. Three 200-watt Sylvania daylight bulbs were mounted, 2.5 feet (76 cm) apart, along the ridgepole of each of the covers. The intensity of artificial illumination at the water surface varied from 24 to 63 foot-candles in each of these tanks.

In these later experiments, water temperature was maintained at one of two levels, 8.5±1° or 16±1°. To obtain the higher temperature, water was heated to 25° and passed through a glass wool filter into a large wooden reservoir (1.5 × 1.5 × 6 feet or 46 × 46 × 183 cm) which was a fractionating column modified after Shephard (1955). The column was filled with stones approximately 13 cm in diameter, and compressed air was bubbled up through an opening in the base of the reservoir. The water in the reservoir was adjusted to the appropriate level to bring the oxygen content of the water issuing from the column to 95% air saturation (8.0 parts per million O_2, 25° C). Cold and warm water were mixed to obtain a temperature of 16±1°.

All the experimental tanks, (both the small ones used in the initial series and the larger ones used in later experiments) were made light-proof by caulking adjoining surfaces and by glueing sponge rubber around the door jambs and bases of the covers. The lengths of the photoperiods were controlled automatically by time switches. Details of the various photoperiodic and thermal conditions will be given in the appropriate places below.

Five days per week the fish were fed a commercially prepared food in the form of quarter-inch (6-mm) pellets manufactured by Glencoe Mills Inc., Minnesota. Although the dietary requirements of trout are not fully known, this preparation seems to be quite adequate in view of the success with which it has been used in different laboratories and hatcheries.

Care was taken to keep the tanks as clean as possible. Waste material at the bottom of the tanks was removed daily, and every 2 or 3 weeks the tanks were thoroughly cleaned.

Unfortunately, mortality was rather high. In each tank usually 6–10 fish per 100 died every month. Some of the fish in each lot were diseased at the time they were received at the laboratory, and despite prophylactic treatment,

which undoubtedly served to reduce losses, the diseases could not be completely eradicated.

Sporadic outbreaks of furunculosis and ulcer disease occurred in almost every tank. If an infected fish was observed, it was immediately discarded and the members of that tank treated with sulfamerizine according to the methods outlined by Snieszko *et al.* (1950). This treatment was most successful in arresting the spread of both diseases. By far the most common disease and, fortunately, one that can be controlled, was an infection by the fungus *Saprolegnia* sp. This was particularly prevalent in fish approaching functional maturity, which are generally debilitated. Infection by the fungus was probably secondary following injuries received through the aggressive behaviour of mature males and through handling during stripping operations. Fish so infected were treated with a 1% common salt solution or with acriflavin in a concentration of 2 mg/l following the techniques given by Davis (1956).

Periodically, water samples were taken from all tanks and analysed for oxygen content using the unmodified Winkler method (Standard Methods for the Examination of Water, Sewage, and Industrial Wastes, 9th ed.). In no case was the oxygen concentration found to be less than 70% of the air equilibrium values.

Sampling of Fish

Fish were collected at random from the tanks and killed by a sharp blow on the head. Each fish was sponged with dry cheesecloth to remove most of the adhering water and weighed to the nearest tenth of a gram. Standard length was measured to the nearest millimetre. This length is defined as the distance between the tip of the snout and the beginning of the caudal fin (i.e., the end of scalation). An incision was made along the mid-ventral line and the gonads, together with the associated mesentries, were removed and placed in Davidson's fixative[4]. To ensure complete penetration, the gonads were allowed to remain in this preservative for at least 3 months.

Samples consisting of 1 male and 1 female fish were collected from each of the tanks at approximately semi-monthly intervals. The rate of sampling was conditioned somewhat by the stage of gonadal maturation of the fish and by the extent of mortality. Thus, samples were only taken every 3 or 4 weeks during the spring months since little development of the gonads occurred during this period. Some fish died as a result of laboratory accidents (water failures, sudden temperature increases owing to a blockage of the cold water line, injuries during handling, etc.). These fish are included in the results reported for each experiment. From time to time, fish were found dead in the tanks and the cause of death could not be determined. Such fish were also included as samples for the relevant experiments if they met the following three criteria: (1) the intestinal tract was filled with partially digested food; (2) the behaviour of the fish (swim-

[4]Composition of Davidson's solution used for the preservation of trout gonads: 1) Ovaries: Solution A for 24 to 48 hours, consisting of 30 cc 95% ethyl alcohol, 20 cc neutralized formalin, 10 cc glycerine, 10 cc glacial acetic acid and 30 cc distilled water. The material was then stored in solution B, which is the same as A but without the acetic acid. 2) Testes: Solutions A and B without glycerine were used as above.

ming, orientation, feeding) had been normal on the day previous to death; (3) there was no indication of severe infection, internally or externally. (If conditions 1 and 2 were fulfilled, mild infections were not considered to have debilitated the fish to the extent of seriously affecting gonadal development.)

Data Collected from Female Trout

The data obtained from trout ovaries were based on macroscopic measurements. A small number of control fish were examined microscopically to familiarize the experimenter with the structure of the gonad. Before proceeding further, it is necessary to give a brief description of the ovarian cycle and to define several terms that are used throughout the text.

Morphology of the ovary. The ovaries are paired, elongate organs lying ventral to the swimbladder in the abdominal cavity. Each is suspended by a double peritoneal fold, the mesovarium, which originates from the parietal peritoneum covering the ventral surface of the swimbladder. A non-functional gonoduct is formed by the backward extension of the peritoneum which also partially envelopes each ovary. Mature ova are discharged from the ovarian lamellae directly into the coelom, and from there pass through a single abdominal pore (occasionally a pair) into a thin walled sac which opens to the exterior on the urinogenital papilla.

Female brook trout that have been reared in hatcheries usually become functionally mature for the first time during the autumn of their second year. When fish are a year old (January), the ovary is filled with a mass of small ova ranging in diameter from 0.1 mm to about 1.0 mm. The ova grow very little during the spring months, but in July a large proportion of them begin to grow rapidly and constitute the maturing class of ova that will be shed in the autumn of the same year. The ova increase in diameter from approximately 1.0 mm in June to more than 3.5 mm in October. Proliferation of new germ cells takes place during the summer months. These are added to the reservoir of small ova that will give rise to mature gametes during succeeding years. The slow growth period of the germ cells, extending from the time of their formation until they have reached a diameter of approximately 1 mm, is usually termed the *primary growth phase*. The subsequent rapid growth period of the ova is generally referred to as the *secondary growth phase* and it is this stage of oogenesis with which the present study is concerned.

The female germ cells, regardless of the oogenetic stage, are referred to as ova throughout this text. The stages of germ cell development will be described in accordance with the terminology used by Vladykov (1956) in which the terms oogonia and oocytes, popular with many workers, are not used.

1) Recruitment stock: ova less than approximately 1 mm in diameter, yolkless, transparent in fresh condition, but opaque in preserved material. These are distributed throughout the ovarian lamellae in clusters between ova of class 2.

2) Maturing ova: diameter of the ovum varies from about 1 to 4 mm. Yolk laden, pale yellow, changing to a deep yellow or orange towards the period of functional maturity; usually opaque, but become transparent at maturity. They tend to be spherical in shape, but are somewhat distorted by crowding.

3) ATRETIC OVA: this class is composed of maturing ova which degenerate during development. (In the literature, these are variously referred to as resorbing ova, degenerating ova, and pre-ovulatory corpora lutea.) They are pale yellow in early stages, but become dark orange as degeneration proceeds; they are opaque and of irregular shape. Since the maturing ova can degenerate at any stage of development, the approximate diameters of the atretic ova may vary up to 4 mm.

In these terms then, two distinct size classes of ova are normally present in the ovary between July and October, 1) the *maturing ova* which increase in size during this period, and 2) the *recruitment stock* which increase in number during this period. In addition, a small number of *atretic ova* is usually present.

MEASUREMENTS MADE ON OVARIAN SAMPLES. Ovaries were sponged with dry cheesecloth to remove excess fixative and weighed to the nearest tenth of a gram. Each ovary was gently broken in half. The layer of ova on the exposed surface of the anterior half was dissected from the ovary and teased apart. From this group, 15 ova were selected. In this manner a 30-egg sample was collected from the ovaries of each female. Prior to the onset of the secondary growth phase, these samples were composed of the largest ova in the recruitment class. Once the secondary growth phase had begun, the teased portion of a gonad was divided into recruitment and maturing classes of ova, and a sample was taken at random from the latter class.

Ova less than 1.3 mm in diameter were measured with a calibrated Whipple disc in the eyepiece of a binocular microscope. The average diameter was calculated from measurements of a sub-sample of 10 ova from each fish.

Plastic blocks with rectangular grooves, ranging from 2 to 5 mm in width, were used to line up ova larger than 1.3 mm for diameter measurements. The ova were freed from adhering connective tissue and were aligned in the appropriate sized groove. The length of the 30-egg sample was measured with a vernier caliper, 3 times for each sample, the ova being reassembled in different sequences for the second and third measurements. The total of the 3 measured lengths, divided by 90, provided an estimate of the average diameter of the ova. (Since the ova were not perfectly spherical, the three linear measurements differed slightly. The maximum difference between the total lengths for any sample never exceeded 3 mm. Thus, the error in calculation of individual diameters was not more than 0.1 mm). The average diameter of the ova was used as an index of the stage of gonadal development of the female fish.

DATA COLLECTED FROM MALE TROUT

Testes were blotted with dry cheesecloth to remove excess fixative. Small testes were weighed to the nearest centigram, and large testes to the nearest tenth of a gram.

Samples of the testes were obtained by cutting a section approximately 12 mm in width from the mid region of the right testis of each fish. Samples from large testes were further subdivided to permit proper histological manipulation. A representative segment was taken from each of the large samples by making 2 cuts, 3 mm to either side of, and parallel to, the sperm duct. The tissues were dehydrated in ethyl alcohol and embedded in paraffin. Sections,

6 microns thick, were cut in a plane which provided a complete or partial cross section of each testis. The preparations were stained with Mayer's haematoxylin and counterstained with light green.

The slides prepared from every testis were studied and classified as belonging to one of 6 maturation stages. To avoid bias, all the slides were scored over a period of several months without knowledge of the date on which the fish were sampled or the particular experiment to which they belonged. A brief description of the stages is given below. A detailed account of the gross and microscopic structure of the testis and of the spermatogenetic cycle is reported elsewhere (Henderson, 1962).

STAGE 1. (mid January to mid March). Period of slow spermatogonial proliferation. Lobules are composed of cysts of spermatogonia only.

STAGE 2. (mid March to late June). Slow phase of spermatogenesis. Formation of spermatogonia continues. A few cysts in the lobules adjacent to the sperm duct undergo spermatogenesis.

STAGE 3. (late June to early August). Rapid phase of spermatogenesis (I). Lobules composed of cysts at various stages of meiosis and spermiogenesis. The lumina contain small clusters of mature sperm.

STAGE 4. (early August to late September). Rapid phase of spermatogenesis (II). Lobules composed of cysts at various stages of meiosis and spermiogenesis. The lumina are tightly packed with mature sperm which begin to fill the efferent ducts.

STAGE 5. (late September to early November). Period of functional maturity i.e., period during which the fish can be stripped, yielding viable sperm. The primary and secondary efferent ducts are filled with mature sperm. Maturation of the remaining spermatocyte and spermatid cysts is completed.

STAGE 6. (early November to mid January). Period of involution. Phagocytes invade the sperm ducts and lobules and ingest the residual sperm. Division of the primordial germ cells begins, so giving rise to the succeeding year-class of spermatogonia.

STRIPPING OF FISH

In this work, a fish was regarded as being functionally mature when ova or spermatozoa (milt) could be obtained by stripping the fish.

When fish in any one of the tanks in a given series of experiments seemed, by the appearance of the gonads of animals that had been sampled, to be approaching functional maturity, a regular program of testing all fish in that series of experiments was begun using conventional stripping ("spawning") methods, the fish being tested at weekly intervals. An experiment was usually terminated when all the fish in it were functionally mature.

As soon as female trout could be stripped, they were removed from the tank and killed.

Male trout usually became mature before females. Once a male could be stripped, it was measured and tagged with a numbered plastic disc. Each fish was then returned to the tank and stripped at weekly intervals until stripping ceased to express milt, or the fish died, or the experiment was terminated. Ordinarily at the end of an experiment, all surviving males were killed and the gonads preserved for histological examination, but after experiments 1–6 most of the mature fish (males and females) were retained for a later experiment.

NORMAL GONADAL CYCLE IN RELATION TO SEASONAL CHANGES OF DAY LENGTH

The following description is based on observations of gonadal samples collected from 3 groups of fish: (1) fish that were sampled at monthly intervals during 1956 to provide material for a preliminary study of the gonads; (2) fish that served as controls to the initial series of experiments carried out during 1957, and which, for convenience, are referred to as Experiment 6; (3) fish that served as controls to the third series of experiments carried out during 1959 and which are referred to as Experiment 16. (The second series of experiments did not include a control group of fish.)

Each group consisted of 50 fish that were 2 years old at the beginning of the observational period in mid winter. In the fish used in 1956 and 1957, gametogenesis was taking place for the first time (i.e. the fish had not become sexually mature during the preceding autumns). In those used in 1959, gametogenesis was taking place for the second time (i.e. the fish had completed one reproductive cycle).

All groups were exposed to natural solar illumination and maintained at 8.5° C.

FEMALE REPRODUCTIVE CYCLE. In the presentation of results, two lines have been used to illustrate the progress of ovarian development throughout this text: a base line to represent the average diameter of the ova during periods in which no growth takes place, and a trend line, drawn by inspection, to illustrate the increase in average diameter of the ova during the secondary growth phase.

Figure 1 illustrates the average diameters of ova in females maintained under control conditions. No growth of the ova took place during the late winter and spring months when the day lengths were increasing from near minimal to maximal levels. The secondary growth phase of the ova began in July, following the summer solstice, and was completed by mid October, soon after the autumnal equinox. During this period, ova of the maturing class increased in diameter from a little more than 1 mm to approximately 3.8 mm. The size of the mature ova from different fish varied between 3.5 and 4.0 mm.

MALE REPRODUCTIVE CYCLE. In all figures concerned with testicular development, the duration of each of the maturation stages is delineated by a horizontal line drawn through a number of points (for summary of stages, see above). Each point represents the developmental stage of a single fish. Stages 1–4 are based on examination of histological preparations and Stage 5 represents the first date on which each individual fish could be successfully stripped. A few of the samples collected from both the control and experimental groups of fish were in Stage 6 (period of involution), but these data are omitted from the graphs since this phase of development has no connection with the problem under consideration.

Figure 2 illustrates the spermatogenetic cycle in fish maintained under control conditions. Examination of this figure shows that spermatogonial proliferation took place at a slow rate throughout the winter months when the day lengths were comparatively short (Stage 1). During the spring, when the

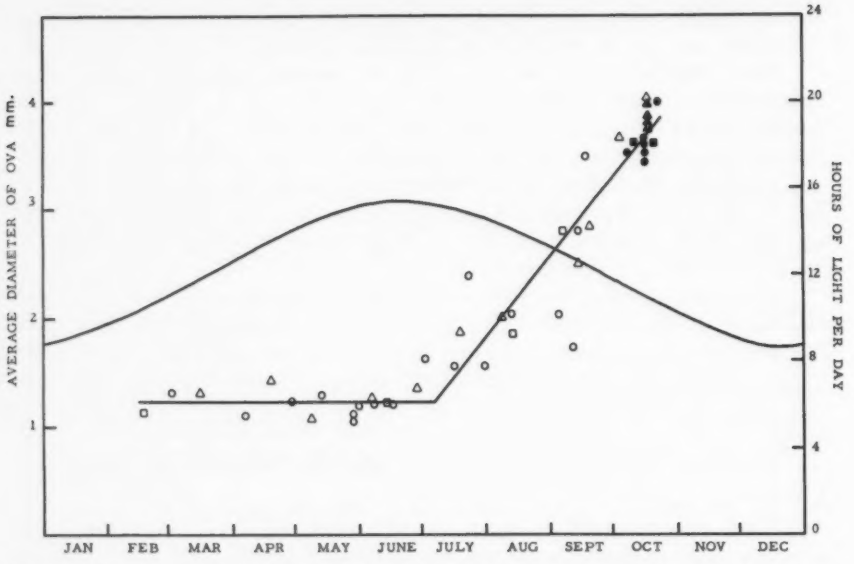

FIG. 1. Normal growth rate of ova. The different shapes of the symbols refer to the 3 groups of fish sampled—*squares*: 1956; *circles*: 1957; *triangles*: 1959. *Open symbols*: immature ova; *solid symbols*: mature ova. Each point represents the developmental stage of an individual fish. The *curved line* describes the normal light cycle at Toronto.

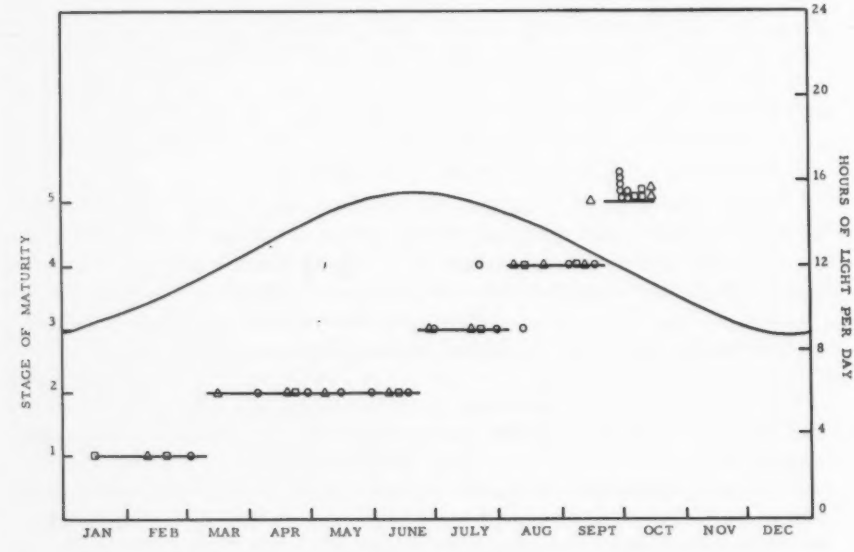

FIG. 2. Normal maturation of the testis. Symbols are as in Fig. 1.

day lengths were increasing to the maximal level, a few cysts underwent spermatogenesis in the lobules adjacent to the sperm duct (Stage 2). The rapid phase of spermatogenesis began at the summer solstice and the entire testis was characterized by intense activity throughout the summer months (Stages 3 and 4). This phase was terminated with the onset of functional maturity at the time of the autumnal equinox (Stage 5).

In brief, it is clear that when fish are maintained under the standard conditions employed in this study, that gametogenetic activity is associated with the decreasing day lengths that follow the summer solstice.

EXPERIMENTS 1–5

The initial series of experiments was undertaken with the assumption that light and temperature play a role in the regulation of the reproductive cycle. The purpose of this series was to determine whether the time of functional maturity could be predicted in terms of an additive effect of the photoperiodic and/or thermal experience of the fish, that is, whether the production of mature gametes is the result of exposure to a certain number of light-hours or day-degrees, or to a combination of some quantities of both of these environmental variables.

At the beginning of these experiments the trout were 2 years old. They originated from a slow-growing hatchery stock of trout, and had not become mature during the autumn preceding the experimental period.

Experimental Conditions

All experiments were begun on March 15, 1957. Prior to this time, the fish had been exposed to natural illumination and held at 8.5°. After March 15, the fish received only artificial illumination except for the brief period each day when the tanks were cleaned and the fish were fed. Each tank contained 50 fish.

Experiment 1. Accelerated light regime, 8.5 and 16° C. On March 15, the artificial photoperiod was set at 12 hours per day, and thereafter was increased at the rate of 1 hour per week, until the length of the light period reached 20 hours per day (May 10). No further change was made for 8 weeks, following which the photoperiod was decreased at the rate of 1 hour per week. On the basis of the hypothesis of summation of light periods, this group of fish was expected to become functionally mature in early September (6 weeks in advance of controls) when the length of the photoperiod had been reduced to 11 hours per day and the fish had received the same total number of light hours as the controls would receive at the normal time of functional maturity on October 15. However, maturation did not occur at this time. Consequently, the light period was further decreased by 1 hour per week to 7 hours per day and then held at that level. The weekly increases and decreases of light were made in 4 instalments of 15 minutes each, and these changes were made alternately at the beginning and the end of a daily light period.

The water temperature remained at 8.5° until June 15, and then was increased to 16° for a period of 2 months. The temperature was reduced to 8.5° during the third week in August.

EXPERIMENT 2. ACCELERATED LIGHT REGIME, 8.5° C. The light treatment in this experiment was the same as that described for Experiment 1. The fish were held at a temperature of 8.5° throughout the experimental period.

EXPERIMENT 3. RETARDED LIGHT REGIME, 8.5 AND 16° C. The fish were exposed to a 12-hour photoperiod of artificial illumination from March 17 to October 12. Subsequently, the photoperiod was decreased at the rate of 20 minutes per week. On the basis of the light summation hypothesis, fish receiving this light treatment were expected to become functionally mature in the latter part of November (6 weeks later than usual) when the photoperiod had been reduced to 10 hours per day and the fish had received the same total number of light hours as controls had received at the normal time of functional maturity on October 15. (This regime was essentially a 12-hour light cycle throughout the period of gonadal development).

The temperature of the water remained at 8.5° until August 1, and then was increased to 16° for the months of August and September. The temperature was decreased to 8.5° during the first week in October. By August 1, the fish in this experiment had received the same total number of light hours as the fish in Experiment 1 had received by June 15 when a similar increase in temperature was made.

EXPERIMENT 4. RETARDED LIGHT REGIME, 8.5° C. The light treatment was the same as that described for Experiment 3. The fish were maintained at 8.5° throughout the experimental period.

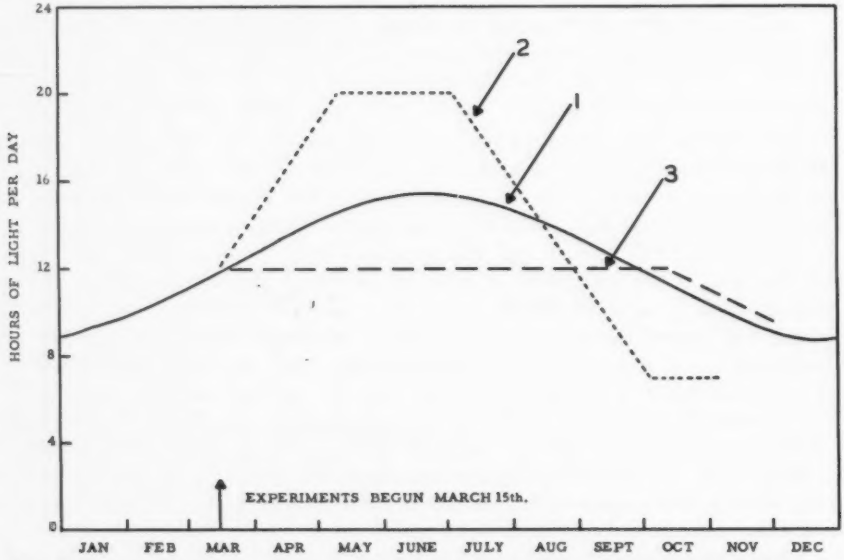

FIG. 3. Experimental light regimes used in Experiments 1–5, together with a curve describing the normal light cycle at Toronto. 1. normal light cycle (Experiment 5); 2. accelerated light regime (Experiments 1 and 2); 3. retarded light regime (Experiments 3 and 4).

EXPERIMENT 5. ARTIFICIAL ILLUMINATION AT NATURAL DAY LENGTHS, 8.5° C. An additional experiment was carried out in which fish were subjected to natural day lengths, but with artificial rather than solar illumination. The length of the daily photoperiod was adjusted 4 times per week to correspond to the natural day lengths occurring at the latitude of Toronto (44° N). Normal day lengths were calculated from the tables of Times of Sunrise and Sunset in "The Observer's Handbook", published by the Royal Astronomical Society of Canada. Throughout this text, all times are given in Eastern Standard Time. The water temperature remained at 8.5° throughout the experimental period.

The experimental light conditions are summarized in Fig. 3, together with a curve depicting the normal light cycle at Toronto.

FEMALE REPRODUCTIVE CYCLE

Figure 4 illustrates the changes in the average diameters of the ova taken from gonads of female trout from Experiments 1–5. Growth of ova in control fish is shown by broken lines.

In fish subjected to the accelerated light regime at 8.5° and 16° (Fig. 4a), the time of onset of the secondary growth phase, rate of growth of the maturing ova, and the period of functional maturity, paralleled the changes observed in control trout.

When fish were exposed to the accelerated light regime at 8.5° (Fig. 4b), the ova began to increase in size at the normal time, and although a number of fish became functionally mature in mid October, several fish could not be stripped until mid November. Since the size of the fully developed ova did not vary with the time of maturity, it seems probable that ovarian development was slightly retarded in some of the fish.

When fish were subjected to the retarded light regime at 8.5° and 16° (Fig. 4c), the secondary growth phase was initiated at the normal time, but seems to have continued at a slightly higher rate than normal with the result that although the fish could first be stripped at the regular time in mid October, the average diameters of mature ova were larger than those observed in control samples.

In the experiment in which fish were held on the retarded light regime at 8.5° (Fig. 4d), no conclusion can be drawn concerning growth of the ova owing to a lack of an adequate number of samples. In this group of fish, the period of functional maturity extended over 7 weeks, some fish having matured a few weeks earlier than normal, and the others several weeks later than normal.

In fish subjected to artificial illumination for natural day lengths and held at 8.5° (Fig. 4e), the growth and maturation of the developing ova did not differ from the results reported for control fish.

MALE REPRODUCTIVE CYCLE

Figure 5 represents the maturation stages of testes collected from male trout of Experiments 1–5 during the months between March and November.

Under the accelerated light regime at 8.5° and 16° (Fig. 5a) or 8.5° (Fig. 5b), males remained in Stage 1 for 2 months longer than controls. Stage 2, although of shorter duration than in the controls, occurred within the usual time period.

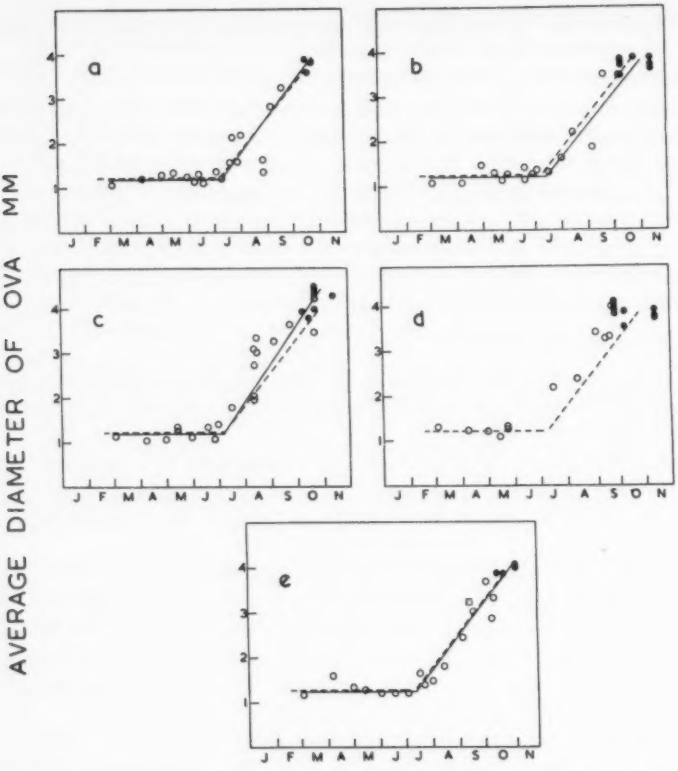

FIG. 4. Rate of growth of ova in fish from Experiments 1–5. *Open circles:* immature ova; *solid circles*: mature ova; *broken lines*: normal growth rate of the ova.

(a) Accelerated light regime, 8.5° and 16° (Experiment 1).
(b) Accelerated light regime, 8.5° (Experiment 2).
(c) Retarded light regime, 8.5° and 16° (Experiment 3).
(d) Retarded light regime, 8.5° (Experiment 4).
(e) Artificial illumination at natural day lengths, 8.5° (Experiment 5).

Stages 3 and 4, comprising the rapid phase of spermatogenesis, occurred normally and the fish could be stripped at the regular time in early October.

When fish were subjected to the retarded light regime at 8.5° and 16° (Fig. 5c) or 8.5° (Fig. 5d), Stage 2, the slow phase of spermatogenesis, took place at the normal time although a few fish were delayed in Stage 1. Stages 3 and 4 were begun several weeks in advance of controls, yet functional maturity was attained at the normal time in both these groups of fish.

Under artificial illumination for natural day lengths and a temperature of 8.5° (Fig. 5e), a few fish persisted in Stage 1 until mid May, but at the same time, some fish were in Stage 2. The remaining stages of the spermatogenetic cycle were concurrent with those observed in the control fish.

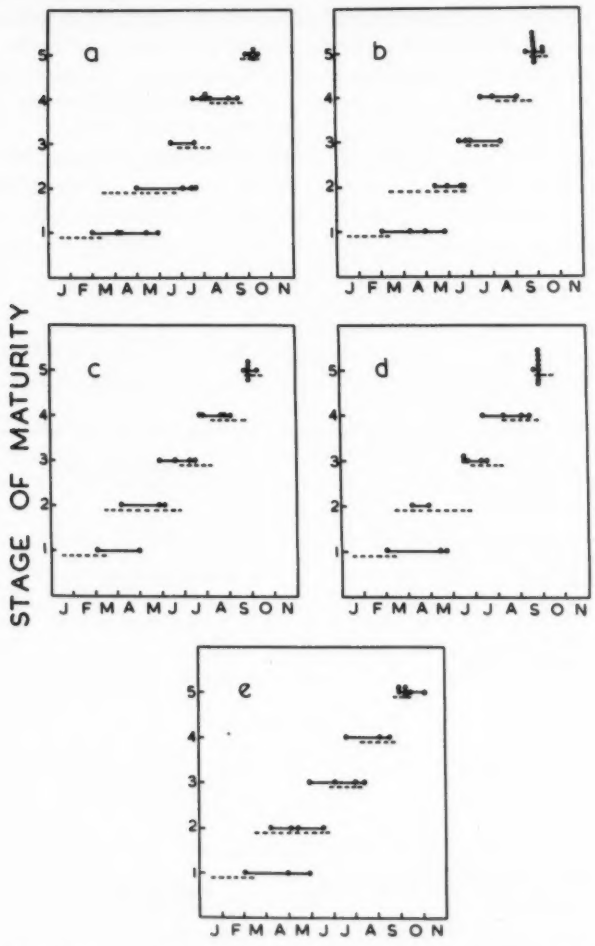

FIG. 5. Gonadal maturation of male trout from Experiments 1–5. The *broken lines* indicate the normal duration of each stage. Experimental details are as in Fig. 4.

TIME OF ONSET OF FUNCTIONAL MATURITY

The periods of time during which male and female trout reached functional maturity in each of the experiments are summarized in Fig. 6.

The extended period of onset of functional maturity in females of Experiment 3 was due to a retardation of one fish. The periods for females of Experiments 2, 4 and 5 appear to have been prolonged, but it is felt that the variation in time of maturity is no more than might be expected among individuals. Figure 4 shows that the variability in the size of the maturing ova was no less than the variability

in time of maturity. I have observed several large stocks of slow growing trout that were becoming functionally mature for the first time, and noted that many of the females could not be stripped until mid November. Thus I conclude that the periods of functional maturity in females of Experiments 1–5 were not significantly different from the period observed in control fish.

The prolonged period of onset of functional maturity in males of Experiment 5 was due to a retardation of one fish and therefore, is not considered to differ significantly from controls. Males in the other 4 experiments became mature within the normal time period. In each experimental group the males became functionally mature slightly earlier than the females.

In the course of stripping male trout at weekly intervals, it was found that milt could be expressed from individual control fish for 7 to 8 consecutive weeks. The viability of the sperm was tested by the "dry fertilization" technique (Davis, 1956) using ova from females which had become functionally mature within 1

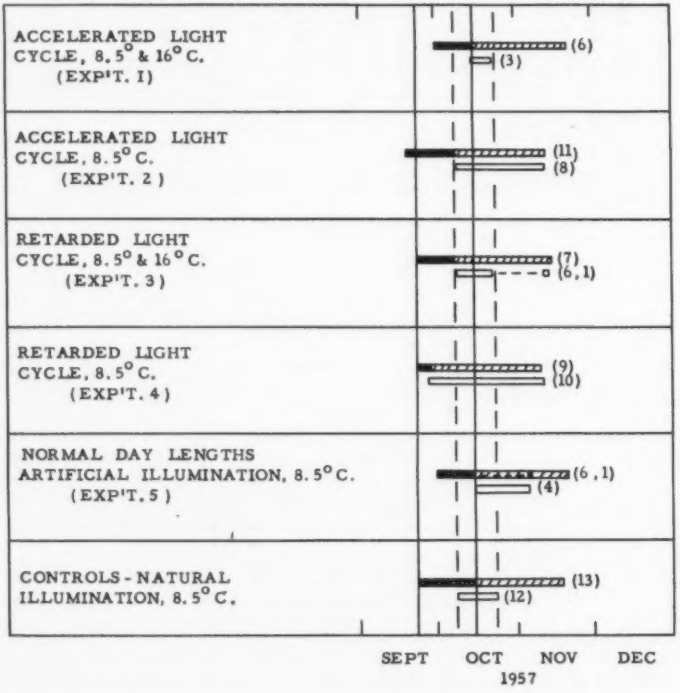

FIG. 6. Time of onset of functional maturity in fish from Experiments 1–5. *Open bars*: periods of time during which females reached functional maturity; *solid bars*: comparable periods for males; *solid plus striped bars*: periods during which males yielded viable sperm (i.e., were functionally mature). *Vertical lines* delineate the times during which males and females normally reach functional maturity (from Fig. 1 and 2). The number of fish used in constructing each bar is indicated in brackets.

week of each test. Ova were successfully fertilized by milt withdrawn from males during the first 6 or 7 weeks following the onset of functional maturity. This would imply that, in captivity at least, the period of functional maturity in individual fish persists for approximately 6 weeks. None of the males in Experiments 1–5 differed from the control fish in this respect, and thus none of the experimental conditions employed in these 5 experiments affected the period of viability of the sperm.

Summary

The light and temperature regimes employed in the foregoing experiments had little, if any, effect on the reproductive cycles of either male or female trout. The experimental groups of fish differed from the controls only in minor details and can be said to have matured normally.

These results indicate that the time required for development of the gonads in brook trout undergoing their first reproductive cycle is not directly determined by the total numbers of hours of illumination received by the fish.

An increase of temperature to 16° during part of the period of germ cell maturation is without any demonstrable effects on gonadal development.

It is not possible to predict the time of functional maturity on the basis of an additive effect on the photoperiodic and/or thermal history of the fish, within the limits of the conditions employed here.

Fish held under normal day lengths, but in artificial light (Experiment 5), did not differ from control fish. Therefore, intensity and probably quality of illumination appear to be without influence on the reproductive cycle of this species (within the limits employed here).

EXPERIMENTS 7–12

The foregoing experiments did not support the conclusion suggested by the investigations of other workers (e.g., Hoover and Hubbard, 1937), that the length of the daily photoperiod played an important role in the regulation of the reproductive cycle of brook trout. Hence more drastic and simpler light regimes were tried, to determine whether any effects could be induced under these conditions. Gonadal response was checked at various phases of the gametogenetic cycle and with several photoperiodic regimes, at 8.5 and 16° C.

The fish used were 2 years old at the time experiments were begun. They had originated from a rapidly growing hatchery stock of fish and had become mature during their second autumn, that is, the autumn preceding the late winter period in which experiments were begun, and hence were in their second reproductive cycle.

Experimental Conditions

Each tank contained 140 fish, which had been exposed to natural solar illumination and held at 8.5° prior to the initiation of experiments in February or March, 1958. The experimental conditions are given in Table I.

During a 20-hour regime, the lights were on from 0200 to 2200 hours, and during a 4-hour regime, from 1000 to 1400 hours. The tanks were open every

TABLE I. Conditions of Experiments 7–12

Experiment No.	Light regime	Temperature
7	Decreased from 11 to 4 hr/day, Mar. 8–Apr. 26	8.5°
11	As above	16°
8	As above, then increased to 20 hr/day, July 23–Aug. 6	8.5°
12	Increased from 10 to 20 hr/day, Feb. 15–Apr. 26	8.5°
10	As above	16°
9	As above, then decreased to 4 hr/day, July 23–Aug. 6	8.5°

day between 1000 and 1400 hours during the experimental period. Thus, some of the fish received both solar and artificial illumination for 4 hours per day, while others received an additional period of 16 hours of artificial light per day. (Although a combination of artificial and natural illumination was used, no significance will be attached to this point since Experiment 5 had shown no effects of intensity and quality of illumination within the limits of the conditions employed in this study.)

A complication of these experiments arose from the fact that in early September a sudden high mortality occurred in fish of Experiments 7, 8, 10 and 12. The cause of death is not known. Most of the fish that died from Experiment 7 and some from Experiments 8, 10 and 12 were sampled and included in the results.

During the period of heavy mortality (1 week), the fish exhibited abnormal orientation and ceased feeding. Gross and microscopic examination of various organs and tissues did not reveal any structural abnormalities or parasitic infections. A full description was sent to Dr S. F. Snieszko of the Microbiological Laboratory, Kearneysville, W. Va. who agreed with the writer's suggestion that death may have been due to a virus infection of the nervous system.

FEMALE REPRODUCTIVE CYCLE

Figure 7 illustrates the growth of ova in fish from Experiments 7–12, compared with normal growth.

EXPERIMENT 7 (Fig. 7a). In fish exposed to 7 weeks of short photoperiods, and low temperature, the secondary growth phase was initiated during May, almost 2 months earlier than usual. The growth rate of the ova was retarded however, and the females did not become functionally mature until the latter part of November.

EXPERIMENT 11 (Fig. 7b). When fish were exposed to 7 weeks of short photoperiods and held at 16° the time of onset and the rate of the secondary growth phase of the ova were normal. However, the time of functional maturity was delayed by 2 to 6 weeks and the average diameters of the mature ova were slightly larger than those observed in the control groups of fish.

TABLE II. Summary of the experiments.

(↗ increasing, ↘ decreasing, → constant)

Year	Experiment Number	Age of fish at beginning of experimental period (years)	Temperature regime (degrees C.)	Light regime (hours per day)	Time of functional maturity - females	Time of functional maturity - males
1957	1	2	8.5° → June 15 ↗16° → Aug. 15 ↘ 8.5° →	12(Mar.15) ↗20(May 10)→ July 4 ↘ 7(Oct.3) →	normal	normal
"	2	2	8.5° →	as above	normal	normal
"	3	2	8.5° → Aug.1 ↗16° → Oct. 1 ↘ 8.5° →	12 Mar.17 → Oct.12 ↘ 20 min. per week →	normal	normal
"	4	2	8.5° →	as above	normal	normal
"	5	2	8.5° →	artificial light, photoperiod same as natural day length	normal	normal
1957	6 (controls)	2	8.5° →	natural day length	normal	normal
1958	7	2	8.5° →	11(Mar.8) ↘ 4(Apr.26) →	retarded	normal
"	8	2	8.5° →	11(Mar.8) ↘ 4(Apr.26) → July 23 ↗20(Aug.6) →	retarded	retarded
"	9	2	8.5° →	10(Feb.15) ↗20(Apr.26) → July 23 ↘ 4(Aug.6) →	advanced (slightly)	advanced
"	10	2	16° →	10(Feb.15) ↗20(Apr.26) →	?[1]	?[1]
"	11	2	16° →	11(Mar.8) ↘4(Apr.26) →	retarded	retarded
"	12	2	8.5° →	10(Feb.15) ↗20(Apr.26) →	retarded	retarded
1959	13	4	8.5° →	9.8(Feb.1) ↗20.5(Mar.28) → Apr.25 ↘ 7(July 11) →	- - -	advanced
1959	14	2	8.5° →	as above	advanced	advanced
"	15	2	16° →	natural day length	probably normal[2]	probably normal[2]
"	16 (controls)	2	8.5° →	natural day length	normal	normal
1958	17	3	8.5° →	12(Mar.15) ↗20(May 10) - → July 4 ↘ 7(Oct.3) →	advanced	advanced

1 None of the fish had become functionally mature by the time the experiment was terminated in the spring of 1959, more than a year after it was begun.

2 The experiment was not completed, but the data suggest that gonadal development was normal.

EXPERIMENT 8 (Fig. 7c). With the same initial conditions as Experiment 7, the secondary growth phase again started about 2 months earlier than usual. However the later increase in photoperiod from 4 to 20 hours was followed by conspicuous alterations of the maturation cycle. During the months of August to November large numbers of atretic ova were found in most of the fish sampled. These were in all stages of disintegration and varied in diameter from 3.0 to 1.5 mm. The class of maturing ova which had begun to develop in May was diminished as a result. At the same time, most of the ovaries examined contained a second, smaller class of maturing ova. These ova varied from 1.4 to 2.0 mm in diameter, and there were several hundreds in each fish[5].

There was a marked gradation in the size of the developing ova in fish examined from late November to January. (This gradation suggests that the ova, comprising the second maturing class, entered the terminal growth phase over a period of a month or more.) Resorption of the ova which had previously constituted the first (or what would normally be the current) class of maturing ova was continuing, but by this time the atretic ova were considerably reduced in size, the maximum diameter being about 2 mm.

During February and March, the appearance of the ovaries was that of control fish in late summer, although it is possible that the recruitment stock of ova was reduced in number. The data suggest that the experimental conditions employed here could produce a late winter or spring spawning stock of fish.

These results are interpreted as indicating a resorption of the current year-class of maturing ova and a stimulation of what would normally be the succeeding year-class of maturing ova, to undergo precocious development. From October on, the results seem orderly, but it should be pointed out that the growth rate of the ova was slower than normal. (In 3 of the fish examined during September, the ovaries did not appear to contain a maturing class of ova. It is possible that no development of their ovaries had occurred, but it seems more likely that the first class of maturing ova had been resorbed and that development of the second class had not yet begun.)

EXPERIMENT 12 (Fig. 7d). In fish maintained under a long photoperiod at a low temperature, the maturing ova appeared to begin the secondary increase in size at the normal time, but it is clear that their growth rate was markedly retarded, and to a greater extent in some females than in others. The results suggest that under these experimental conditions, females would reach functional maturity in late winter.

EXPERIMENT 10 (Fig. 7e). The secondary growth phase began at the regular time in fish maintained on a long photoperiod at 16°. Initially, growth of the ova seemed to be normal, and indeed one exceptional fish became functionally mature in October.

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[5]When two distinct size classes of maturing ova were present, the diameters of the ova in both classes were measured and the averages of each were included in the relevant graphs. When a gradation in the size of the developing ova occurred, only the largest ova were selected for diameter measurements.

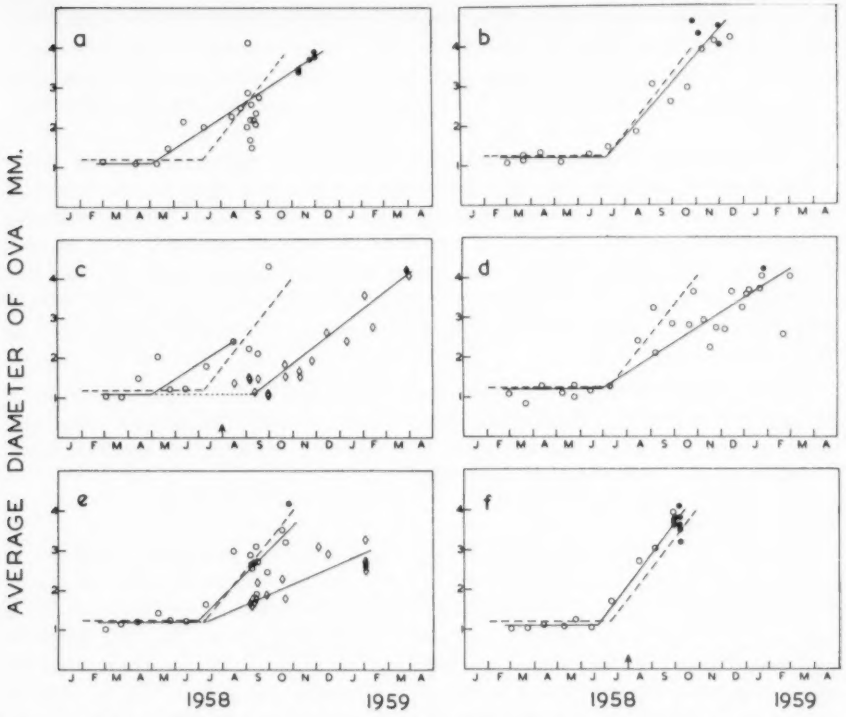


FIG. 7. Rate of growth of ova in trout from Experiments 7–12. *Open symbols:* immature ova; *solid symbols:* mature ova. *Broken lines:* normal growth of the ova. In (c) and (e), *circles* represent the first class of ova to enter the secondary growth phase, while *diamonds* are the second class of maturing ova. See Table I for the temperature and lengths of the photoperiods in each experiment. Times of abrupt change of photoperiod are marked by an arrow in (c) and (f).

In almost every ovary collected during September and October, the current year-class of maturing ova was developing normally, but an additional group of several hundred smaller ova had also entered the secondary growth phase and ranged in diameter from 1.5 to about 2.0 mm. Thus, the ovaries contained two distinct size classes of maturing ova as well as the recruitment stock (see footnote 5).

From December on, large numbers of atretic ova were observed in all of the ovaries examined. The degenerating ova varied from 3.0 to 1.5 mm in diameter and were in all stages of resorption. At the same time, the ovaries contained a large class of maturing ova. The diameters of these ova varied from about 2.0 to 3.0 mm but, in each ovary, a large proportion fell in the highest part of this range. Since the average diameters of the largest ova were less than the average diameters of the larger size class of ova that was developing in October, and in view of the large numbers of atretic ova, it seems likely that the maturing ova, present from December on, belonged to the class which began development in

October, and that the atretic class was composed entirely or almost entirely of the ova which had begun to develop in July. When the experiment was terminated in February, it was apparent that the recruitment stock was markedly reduced in number and that the ova in the recruitment stock were smaller than normal.

Evidently the effect of this light and temperature regime was to bring about a resorption of what would normally be the current year-class of maturing ova at an advanced stage of development. At the same time, these conditions apparently caused a stimulation in growth of the ova which would not normally develop until the following year. It would be interesting to know whether this latter group of ova would eventually complete maturation or whether atresia would occur at a stage comparable to that observed in the preceding year-class of maturing ova.

EXPERIMENT 9 (Fig. 7f). When fish were exposed to a long, followed by a short, photoperiod at 8.5°, development of the maturing ova appeared to take place at approximately the normal rate. The fish could be stripped in early October, a week or two earlier than usual.

MALE REPRODUCTIVE CYCLE

Figure 8 illustrates the stage of gonadal maturation in relation to time, in males sampled from Experiments 7–12, as compared with the normal situation. In all 6 experiments Stage 1 continued for approximately 2 months longer than normal, while with the possible exception of Experiment 8 (Fig. 8c), Stage 2 appears to have occurred within the regular time period. It is possible than an overlap between Stages 1 and 2 normally occurred under standard or control conditions, but does not appear in the present results because of the small number of fish examined. Hence it seems unlikely that the extensions of Stage 1 observed in Experiments 7, 9, 10, 11 and 12 are of any significance. On the other hand, the prolongation of Stage 1 in Experiment 8 may well be significant, in view of the pronounced delays which occurred in succeeding stages.

Later stages of the maturation cycle, involving the rapid phase of spermatogenesis (Stages 3 and 4) and the period of functional maturity (Stage 5) were affected to various extents as described below.

EXPERIMENT 7 (Fig. 8a). , With a light regime of 4 hours per day, Stages 3 and 4 occurred at approximately the normal time at 8.5°. The males attained functional maturity from late August to mid October, and therefore the terminal phase of gonadal development must have been accelerated in some fish.

EXPERIMENT 11 (Fig. 8b). At 16° the rapid phase of spermatogenesis was somewhat retarded (Stages 3 and 4). The period in which males could be stripped for the first time (Stage 5), extended from mid September to mid December, although most of the fish became mature at the end of October, several weeks later than normal.

EXPERIMENT 8 (Fig. 8c). Marked retardation of gonadal maturation resulted when fish were transferred from a short to a long photoperiod in mid summer. Stages 3 and 4 were delayed in most of the fish by 3 months, in fact

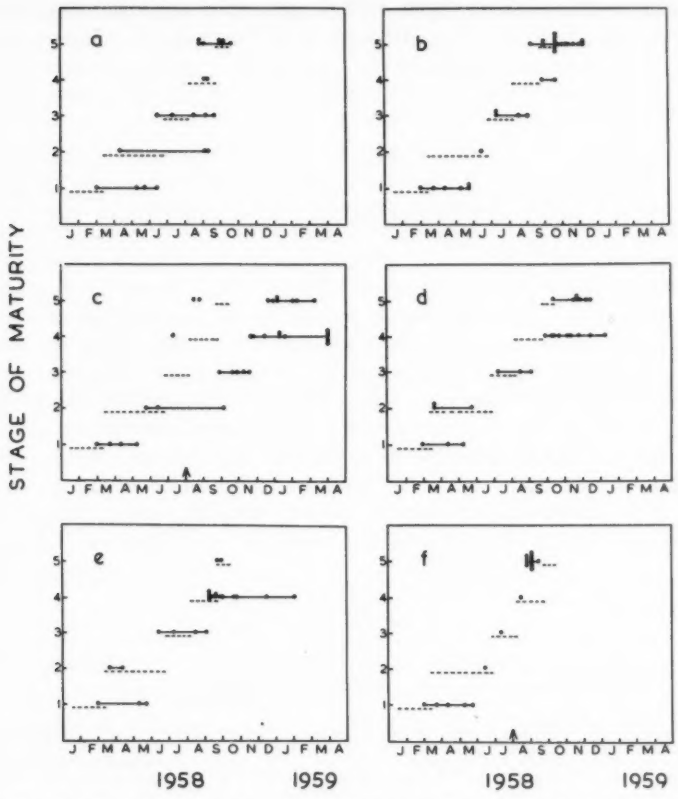


FIG. 8. Gonadal maturation of male trout from Experiments 7–12. *Broken lines*: normal duration of each stage. See Table I for the temperature and lengths of the photoperiods in each experiment.

there were still fish in Stage 4 when the experiment ended on April 1, 1959. Functional maturity was delayed by at least 3 to 5 months. Histologically the testes gave no evidence of a degeneration of one year-class of germ cells and an initiation of a new one, so there is no doubt that in most instances these stages were prolonged. Three out of 29 fish did reach Stages 4 or 5 during mid summer of 1958, but this response was by no means typical.

EXPERIMENT 12 (Fig. 8d). With 20 hours light, at 8.5°, Stage 3 was slightly prolonged and Stage 4 began 1 month later than usual and continued for at least 3 months. The males did not become functionally mature until late November and early December.

EXPERIMENT 10 (Fig. 8e). With the long light periods and a temperature of 16°, Stage 3 was completed normally. Stage 4 began within the regular time period, but continued for at least 4 months longer than normal. The experiment

was terminated in February 1959. With regard to the 2 males assigned to Stage 5, neither fish attained functional maturity in the manner characteristic of this species. Stripping was successful only during the first 2 of many weeks that it was attempted and the amount of milt obtained on both of these occasions was unusually small.

EXPERIMENT 9 (Fig. 8f). With 4 hours illumination following 20 hours, starting at the first of August, the latter part of the rapid phase of spermatogenesis was probably accelerated since the fish could be stripped in late August, 1 month in advance of the normal time.

TIME OF ONSET OF FUNCTIONAL MATURITY

Figure 9 summarizes the period of time during which male and female trout become functionally mature in Experiments 7–12. The data for females in Experiments 8 and 12 consist of single fish in both cases. Each female became functionally mature at the time which would be expected on the basis of the growth rate of the ova (Fig. 7c, d); hence the time at which each matured is a reliable indication of the period of functional maturity in females maintained under the relevant conditions. In Experiment 10, 2 males and 1 female became mature at the normal time, whereas the rest of the fish never reached functional maturity although the experiment was continued for more than a year. The

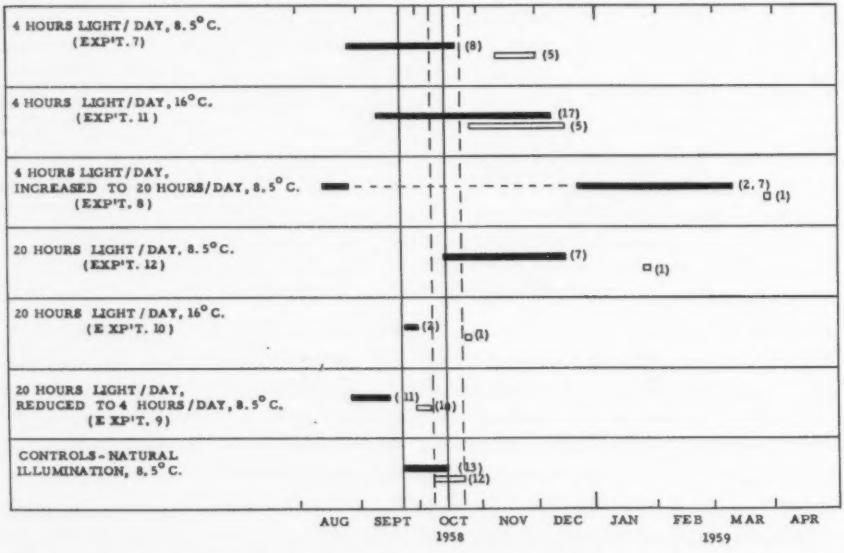


FIG. 9. Time onset of functional maturity in trout from Experiments 7–12. *Solid bars*: males; *open bars*: females. Data for each group of males represent only the period of time during which they reached functional maturity and not the full extent of the period in which they were functionally mature. *Vertical lines* delineate the times during which males and females normally reach functional maturity (from Fig. 1 and 2). The number of fish used in constructing each bar is indicated in brackets.

data from these 3 fish are included in Fig. 9 for the sake of completeness, but these results do not represent the typical gonadal response.

The effect of a 4-hour light regime was to retard the time of functional maturity in females held at 8.5° (Experiment 7), and in both males and females that had been maintained at 16° (Experiment 11). At 8.5° a 4-hour photoperiod during spring and early summer, followed by a 20-hour period, delayed the time of functional maturity markedly in both sexes, and it is reasonable to suppose that this regime could produce a spring-spawning stock of trout (Experiment 8).

A photoperiod of 20 hours per day (Experiment 12) delayed the time of functional maturity by 2 to 3 months at 8.5°. Under the same light regime at 16°, gonadal development had not been completed in most of the fish when the experiment was terminated in April, more than a year after it had been begun (Experiment 10). A 20-hour photoperiod during the spring and early summer, followed by a 4-hour photoperiod during the succeeding months (Experiment 9) may have stimulated maturation slightly since the fish could be stripped a few weeks in advance of the normal time.

In every experiment except No. 10, most of the functionally mature males could be stripped for 6 or more consecutive weeks.

Samples of mature ova and milt from several fish in each of Experiments 7, 8, 9, 11, and 12 were tested for fertility. In every test group, at least 95% of the ova were fertilized.

EXPERIMENTS 13 AND 14

In 1957, 2-year-old maturing trout were subjected to an accelerated light regime (Experiments 1, 2) with the expectation, based on the results of previous workers (Hoover and Hubbard, 1937), that the fish would become functionally mature in advance of the normal time. However, gonadal development was not accelerated and the fish became mature at the regular time in mid October.

An additional experiment (No. 17) was carried out during 1958 that is not reported in detail in this text. Three-year-old adult fish that had been retained from Experiments 1–6, were subjected to exactly the same light and temperature conditions during 1958 that had been used in Experiment 2 during 1957 (accelerated light regime, 8.5°). The small number of fish precluded sampling throughout the experimental period and data were obtained only concerning the time of functional maturity. In contrast to the fish in Experiment 2, which became mature at the normal time in October, all males (12) in this experiment became functionally mature in mid August and all females (3) in late August.

There are two differences between the fish used in Experiments 1 and 2 and those used in Experiment 17: 1) The fish used in Experiments 1 and 2 were not sexually mature, i.e., had not completed one reproductive cycle, while the fish used in Experiment 17 had completed one reproductive cycle; 2) The fish in Experiments 1 and 2 were 3 years old, the fish in Experiment 17, 3 years old. These differences suggested that the gonadal response to an accelerated light regime might depend on whether or not the fish had become sexually mature prior to the administration of the experimental light conditions, or else on the age of the fish. To determine which of these two factors could account for the

different experimental results, a group of 2-year-old fish which had become sexually mature during the previous autumn was subjected to an accelerated light regime (Experiment 14). In addition, a group of 4-year-old males that had become sexually mature in their second year was utilized in a parallel experiment (Experiment 13).

Experiment 14 involved 65 large, 2-year-old fish (males and females) that had come from a rapidly growing hatchery stock of trout. These fish had become sexually mature in 1958 and thus were in their second reproductive cycle. Experiment 13 involved 20 4-year-old adult males that had become sexually mature in 1957 and thus were in their third reproductive cycle.

Experimental Conditions

Experiments 13 and 14 were carried out during 1959. Beginning February 1, the light period was increased each week at the rate of 1 hour per day over the

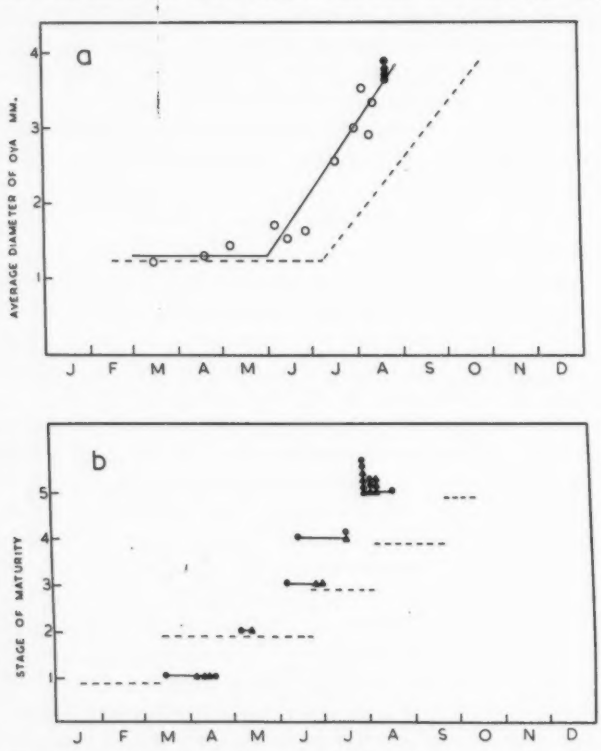


Fig. 10. **a.** Rate of growth of ova in fish from Experiment 14. Fish exposed to an accelerated light regime at 8.5°. *Open circles*: immature ova; *solid circles*: mature ova. **b.** Gonadal maturation of male trout from Experiments 13 and 14. Fish exposed to an accelerated light regime at 8.5°. *Diamonds*: Experiment 13; *circles*: Experiment 14. In both panels the normal gonadal cycle is shown by the broken lines.

natural day lengths, until the photoperiod had reached 20.5 hours per day (March 28). This level was maintained for 4 weeks. Starting April 25, the light period was decreased at the same rate to 7 hours per day (July 11), and then held at this level until the fish became functionally mature. During the time the experimental photoperiods were in excess of natural day lengths, the fish received both artificial and solar illumination, but in the decreasing phase when the photoperiods became less than natural day lengths, the lids of the tanks were closed and the fish received artificial illumination only.

The water temperature remained at 8.5° throughout the experimental period. Prior to the experimental period, all fish were held at 8.5° and exposed to natural illumination.

Female Reproductive Cycle

When adult females were exposed to an accelerated light regime at 8.5°, growth of the ova began at least 1.5 months earlier than usual (Fig. 10a). The rate of growth appeared to be normal, with the result that the fish became functionally mature in late August, 7 weeks before the regular time.

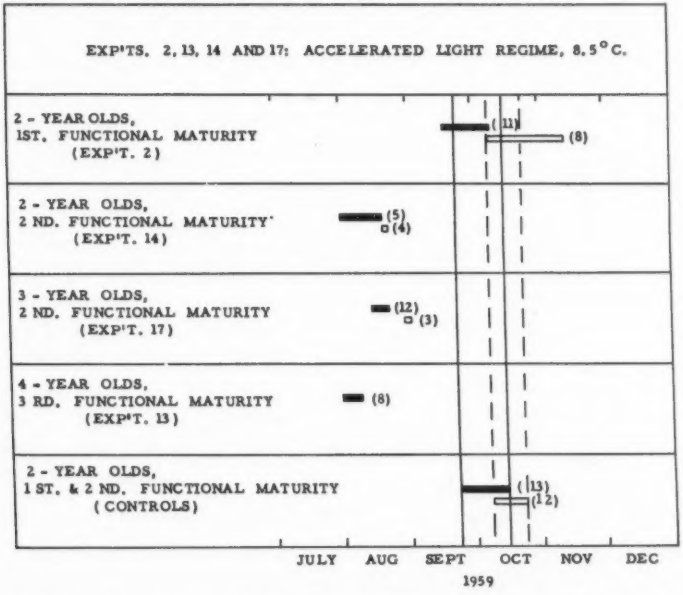


FIG. 11. Time of onset of functional maturity in trout from Experiments 2, 13, 14 and 17. *Solid bars*: males; *open bars*: females. Data for each group of males represent only the period of time during which the males reached functional maturity and not the full extent of the period in which they were functionally mature. *Vertical lines* delineate the times during which males and females normally reach functional maturity (from Fig. 1 and 2). The number of fish used in constructing each bar is indicated in brackets.

Male Reproductive Cycle

Males were in Stages 3 and 4 several weeks before the normal time, and reached functional maturity in late July and early August, approximately 2 months before the regular time (Fig. 10b).

Time of Onset of Functional Maturity

Figure 11 compares the results of 4 experiments that involved similar light regimes. An accelerated light regime induced early gonadal maturity in fish undergoing the second reproductive cycle (Experiments 14 and 17), or the third cycle (Experiment 13), but this regime had no such effect on fish that were completing the first reproductive cycle (Experiment 2). Thus the gonadal response to an accelerated light regime depends on whether or not the fish have become sexually mature previously, and not on the age of the fish.

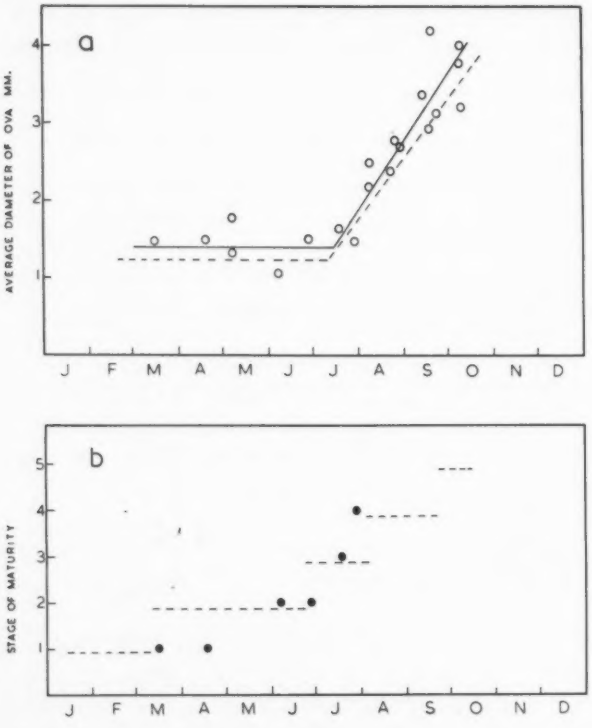


Fig. 12. **a.** Rate of growth of ova in trout from Experiment 15. Fish exposed to solar illumination and held at 16°. **b.** Gonadal maturation of male trout from Experiment 15. Fish exposed to solar illumination and held at 16°. In both panels the normal gonadal cycles are shown by broken lines.

The above finding clarifies what had earlier seemed to be a contradiction between the results of Experiments 1 and 2 and those of Hoover and Hubbard (1937), Hazard and Eddy (1951) and Corson (1955). Using an accelerated light regime, these workers had succeeded in advancing the time of functional maturity in 2-year-old fish. However, they employed only sexually mature fish that had completed one reproductive cycle.

EXPERIMENT 15

Sixty-five 2-year-old adult fish were used in this final experiment, which tests the effect of 16° temperature on trout held under normal day lengths. The fish originated from the same stock as those used in Experiment 14.

Experimental Conditions

Fish were exposed to solar illumination and acclimated to 16° during the first week of February in 1959 and held at this temperature until the experiment was terminated.

Female Reproductive Cycle

Development of the maturing ova at 16° paralleled that of control fish at 8.5° (Fig. 12a). The number of fish available did not allow completion of this experiment, so unfortunately no data are available concerning the time of functional maturity.

Male Reproductive Cycle

Although only a limited number of fish were examined, Fig. 12b suggests that testicular development was normal in fish maintained at 16°.

DISCUSSION. I. REGULATION OF THE REPRODUCTIVE CYCLE

The discussion below is largely based on the results from Experiments 7–12, involving adult trout, but reference is made to evidence from other experiments where pertinent.

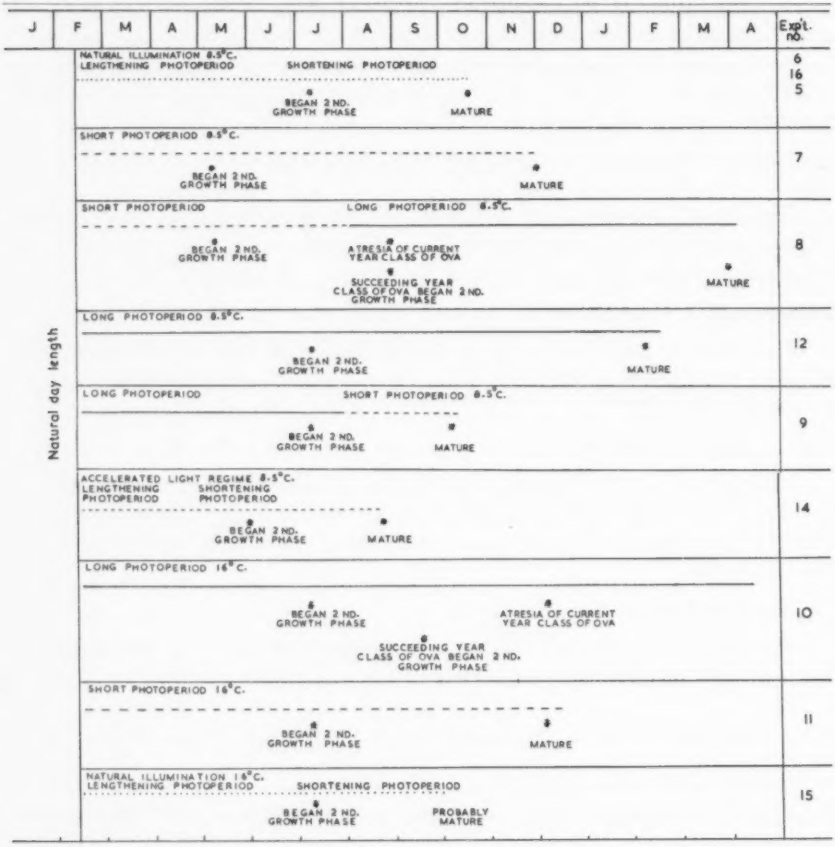
It may be stated at once that there is no evidence from any of the experiments to support the initial suggestion that time of functional maturity might be predictable on the basis of an additive effect of the photoperiodic and/or thermal experience of the fish.

The Ovarian Cycle of Brook Trout

The secondary growth phase of the ova normally begins in early July, following the summer solstice, and is completed by mid October. During the months from July to October the ova grow rapidly and increase in diameter from a little more than 1 mm to about 4 mm.

Changes in the normal cycle of ovarian development were brought about by various experimental light regimes at 8.5°. The relevant experiments, summarized in Table III, suggest that ovarian maturation of fish may be regulated by fluctuations of day length. By what mechanism might this be achieved?

TABLE III. Summary of the effects of light and temperature on female trout.



The secondary growth phase of the ova normally begins soon after the summer solstice when day lengths are starting to decrease (Experiments 5, 6, 16). However, it seems highly improbable that initiation of gonadal development is primarily stimulated by the small reduction in day length (not more than 30 minutes) which occurs during the brief interval elapsing between the time of maximum day length (June 21) and the time of onset of gonadal activity (1–2 weeks later), because when fish were exposed to long photoperiods during late winter, spring and early summer, the secondary growth phase was initiated at the normal time (Experiments 9, 12).

Precocious onset of ovarian development could be induced by subjecting fish to short photoperiods during the late winter and spring months (when day lengths are normally increasing, as in Experiments 7 and 8) or by exposing them to an accelerated light regime in which the increasing and decreasing phases of

the daily light period preceded the normal changes in day length (Experiment 14). Thus, while short photoperiods during the late winter and spring months or an accelerated light regime can hasten the initiation of gonadal activity, this stage is apparently not normally dependent upon decreasing day lengths.

Once the secondary growth phase had started, the rate of ovarian development was retarded either by continuous long or by continuous short photoperiods, if these regimes were begun in late winter with fish that had previously been exposed to natural illumination (Experiments 7, 12). When, however, fish were subjected to long photoperiods during late winter, spring and early summer, and were subsequently exposed to short photoperiods, the growth rate of the ova was accelerated by comparison with that in fish maintained under continuous long or short photoperiods; in fact, the growth of the ova approximated the normal rate (Experiment 9). The stimulating effect of short photoperiods on the terminal part of the growth phase only occurred if the fish were exposed to long photoperiods during the early stages of the secondary growth phase.

These results suggest that the normal growth rate of the ova is dependent upon exposure of the fish to long photoperiods followed by short ones. This conclusion is supported by Experiments 14 and 17, in which it was shown that functional maturity could be induced several months before the regular time by subjecting adult trout to increasing and decreasing photoperiods in advance of the normal solar changes. Under these conditions, the secondary growth phase was initiated earlier than usual and the growth rate of the ova was normal. Early gonadal maturity is the result of an early onset of the secondary growth phase. No experimental conditions were found that would appreciably accelerate the growth rate of the ova.

Since the growth rate of the ova was normal only when fish were exposed to a light regime of long, followed by short, photoperiods, it may be that under natural conditions the rate of growth of the ova is regulated by the shortening day lengths of summer, but this regulation is conditional upon effects produced by the long day lengths of late spring.

In Experiment 8 fish were exposed to short photoperiods during late winter, spring and early summer, followed by long photoperiods. The short photoperiods induced an early onset of the secondary growth phase; but the long photoperiods in midsummer (when day lengths are normally decreasing) produced even more striking changes in the ovarian cycle — namely, precocious development of what would normally be the succeeding year-class of maturing ova and resorption of the current year-class. It is possible that the long photoperiods provided the same stimulus to gonadal development as that which may normally be exerted by the increasing day lengths of winter and spring, namely the initiation of the secondary growth phase in a large proportion of the recruitment stock of ova. Since the development of the new class of ova was accompanied by degeneration of the old class, the situation is analogous to a premature termination of one reproductive cycle and initiation of another.

Experimental work on the role of temperature in the ovarian cycle was limited to a study of the effects of 16° in comparison with 8.5° on fish exposed to

natural illumination or to continuous long or short photoperiods. Using a temperature of 16°, rather than 8.5°, there was no effect on the development of the ova in fish which were exposed to natural illumination (Experiment 15). Therefore the rate of gametogenesis, under natural day lengths, is probably independent of temperature within that range. Under natural conditions it seems likely that the role of temperature, if any, is only minor or supplementary.

However, temperature was not without effect when fish were exposed to continuous long or short photoperiods. When fish were exposed to short photoperiods at 16°, the secondary growth phase began at the normal time; whereas at 8.5° gonadal development started about 2 months earlier than usual (compare Experiments 11 and 7). In fish held under short photoperiods at either of these temperatures the time of functional maturity was delayed to the same extent (1 month), but the retardations were brought about in different ways. At 16° the growth rate of the ova approximated the normal rate, but the ova continued to grow for a longer period than usual and the size of the mature ova was larger than normal, while at 8.5° the growth rate of the ova was markedly retarded.

When fish were subjected to long photoperiods at either 16° or 8.5° the secondary growth phase began at the normal time (Experiments 10, 12). However at 16° the growth rate of the current year-class of maturing ova was retarded from the first. Later on these eggs were resorbed, at the same time as the succeeding year-class of maturing ova underwent precocious development. It is not known whether oogenesis could be completed under these experimental conditions. At 8.5°, the growth rate of the current year-class of maturing ova was retarded and the fish became functionally mature in mid winter; there was no atresia and no precocious development of a new class of ova.

The significance of these results is not understood at the present time and it is evident that more work on light and temperature will be necessary before any interpretations can be offered.

The Testicular Cycle of Brook Trout

Exposure of male trout to long or to short photoperiods at either 8.5° or 16° did not appreciably effect the development of the testis up to Stage 3 (Experiments 7–12). Stage 3, the first half of the rapid phase of spermatogenesis, occurred at the normal time in fish maintained on any of the photoperiodic or thermal regimes, with one exception: it was prolonged by the influence of long photoperiods following exposure to short photoperiods at 8.5° (Experiment 8).

Stage 4, the second half of the rapid phase of spermatogenesis, normally takes place at the latitude of Toronto when day lengths are decreasing from 13.5 to 12 hours per day. Completion of Stage 4 was delayed in fish maintained under (1) continuous long photoperiods at 8.5° and 16° (Experiments 12, 10); (2) continuous short photoperiods at 16° (Experiment 11); or (3) short photoperiods, followed by long photoperiods at 8.5° (Experiment 8). (No experiment was performed with short photoperiods followed by long photoperiods at 16°.) The histological appearance of the testes was normal and a retardation of the time of functional maturity was due chiefly to a delay in spermiation. These results

suggest that the terminal phase of testicular maturation may be regulated by decreasing day lengths and low temperatures under natural conditions.

Although the cyclic changes of the testis are correlated with natural variations of day length and possibly of temperature, the experimental evidence suggests that most of the developmental stages of the testis are largely independent of these two variables. Only the rapid phase of spermatogenesis, particularly the terminal portion, has been accelerated or retarded, following exposure of fish to extreme photoperiods and temperatures of either 8.5° or 16°.

In contrast to the maturation cycle of the female germ cells, which can be modified to a considerable extent by experimental conditions of light and temperature, the maturation cycle of the male germ cells appears to be relatively stable. Harrington (1959b) has pointed out that in fish, " . . . environmental influences on the sex cycle are reflected with greater dependability and particularity in the ovary than in the testis".

Reproductive Cycles in Fish

It is difficult to relate and compare the results from the present study with those obtained by other investigators. In the first place, previous work on teleosts that spawn during the autumn has been concerned only with the time of functional maturity and no attention has been directed to the progressive phases of gametogenesis. Secondly, the multifarious results of investigations with spring-spawning teleosts require lengthy qualifications. The majority suffer from the fact that the experiments were not sufficiently long and did not cover all phases of the maturation cycle. Accordingly, this discussion will be restricted to selected reports which are of particular relevance.

In brook trout, *Salvelinus fontinalis*, functional maturity can be induced several months before the normal time by subjecting fish to a light scheme of increasing and decreasing photoperiods in advance of the normal solar changes (Hoover and Hubbard, 1937; Hazard and Eddy, 1951; Corson, 1955). Similar results have been obtained by Kingsbury (1952) with *Salmo trutta*. Functional maturity of *S. fontinalis* (Hazard and Eddy, 1951) and *Oncorhynchus nerka* (Combs *et al.*, 1959) can be hastened by 3 or 4 weeks merely by reducing the natural day lengths of late summer. Conversely, if several hours of artificial light are given in addition to the natural day lengths in late summer, functional maturity of *S. fontinalis* is delayed by 6 weeks (Allison, 1951; Hazard and Eddy, 1951). A longer delay was observed in an analogous experiment in the present study, in which fish were exposed to continuous long photoperiods of 20 hours per day (Experiment 12).

Atz (1957) has stressed the possibility that the gonadal response to a particular set of environmental conditions may vary with the phase of the reproductive cycle. Bullough (1939) found that in female *Phoxinus laevis* high temperatures alone accelerate the initial stages of the secondary growth phase of the ova, but that long photoperiods are necessary for further growth. Similarly, in the males a high temperature alone leads to an increase in the number of primary spermatocytes, but completion of spermatogenesis depends upon the administration of

both long light periods and high temperatures. Verhoeven and van Oordt (1955), Baggerman (1957) and Harrington (1959b) have reported similar results in *Rhodeus amarus*, *Gasterosteus aculeatus* and *Fundulus confluentus*, respectively.

The present study clearly indicates that the gonadal response to the same conditions of light and temperature varies according to the phase of gonadal development. A short photoperiod coupled with a low temperature during the spring months induced a precocious onset of the secondary growth phase, but retarded the subsequent growth rate of the developing ova, particularly in the terminal phase (Experiment 7). Obviously a short photoperiod may stimulate one phase of the reproductive cycle and retard another. The results reported here show that this is an oversimplification, however, for the effect of a given photoperiod on one phase can depend on the photoperiod to which the fish has been exposed during a previous phase. Thus, in my experiments ovarian development was retarded by short photoperiods in late summer if the fish had been exposed to short photoperiods during spring and early summer, but was stimulated by short photoperiods in late summer if the fish had been exposed to long photoperiods in spring and early summer (Experiments 7, 9). In any long-term experiment, the effect of a given level of an environmental variable, such as the photoperiod, must not only be qualified with respect to the particular phase of gametogenesis that is in progress at the time, but it must also be described in terms of the level of that variable in effect during earlier stages of the reproductive cycle, whether or not this previous level has any demonstrable effects (compare also Experiments 12 and 9, 7 and 8, 8 and 12). This point has not been recognised by previous investigators owing to the brevity or to the design of their experiments.

A number of workers have also shown that certain light and temperature conditions stimulate the various phases of gonadal development, and have stressed the importance of these factors under natural conditions (Burger, 1939b; Merriman and Schedl, 1941; Verhoeven and van Oordt, 1955; Baggerman, 1957; Harrington, 1957, 1959b). The conclusions reached by these authors are based on experiments of relatively short duration. If fish were treated with a particular light and temperature regime, and if little or no progress of gametogenesis was observed within several months, it was assumed that gonadal maturation would only proceed to a certain stage under these conditions. If, on the other hand, a particular set of conditions stimulated rapid development, there was a tendency to assume that these factors were necessary for development. In view of the results from the present study, it is possible that the various workers might have placed less emphasis on the absolute effects of light and temperature in governing the reproductive cycle had they allowed their experiments to continue for many months. In the present study, the experimental conditions did not obliterate the reproductive cycle, they merely modified it.

Brook trout are convenient laboratory fish since they will complete gametogenesis under the simple conditions in which they are usually held. It was fortunate that this species was used in the present study. Many species of fish require undefined conditions to complete oogenesis and spermatogenesis. It

would be interesting to know whether brook trout, in which germ cell maturity had been experimentally induced at unusual times of the year, would spawn if subsequently released into natural waters. Such fish would provide intriguing material for those interested in the factors controlling the initiation of reproductive behaviour and spawning.

Fecundity counts were made on the ovaries collected from every female trout. These results will be presented elsewhere, but none of the experimental conditions employed had any effect on the relation between fecundity and fish length.

DISCUSSION. II. THE MECHANISM OF GONADAL RESPONSE

The demonstration that reproductive activity can be modified by external factors inevitably raises questions concerning the mechanism by which such effects are achieved. Recent work on the control of endocrine function provides some interesting avenues for speculation.

As is well known, reproductive activity is controlled by gonadotrophic hormones produced in the anterior pituitary gland. The influence of the external environment on reproductive processes is believed to be brought about through changes in the quantity of gonadotrophins released from the anterior pituitary.

In the present experiments, a delay in the time of functional maturity in female trout resulted from a retardation of the time of onset or rate of development of the ova or from a resorption of one year-class of maturing ova and the slow growth of another year-class of maturing ova. Once the secondary growth phase was completed (as judged by the diameters of the ova), the germ cells were discharged into the coelomic cavity and the fish could be stripped.

A delay in the time of functional maturity in male trout was brought about by an effect which was apparently induced after most of the germ cells had completed spermatogenesis. When male trout were subjected to long photoperiods at 8.5° or 16° during the late summer months, the period of functional maturity, Stage 5, was delayed (Experiments 8, 10, 12). This retardation was principally due to a prolongation of Stage 4, the terminal portion of the rapid phase of spermatogenesis. Most of the germ cells complete maturation during Stage 4 and the lumina of the lobules become tightly packed with spermatozoa. Spermatogenesis of the remaining cysts is completed in the course of Stage 5 and during this period both the lumina and the efferent ducts are filled with mature sperm. The transition from Stage 4 to Stage 5 chiefly involves the movement of sperm from the lobules into the efferent ducts. Retardation of functional maturity under long photoperiods seems therefore to result from an inhibition of the mechanism by which sperm are released from the testicular lobules, i.e., spermiation.

The mechanism of spermiation in vertebrates has been practically ignored although some attention has been given to the parallel process of ovulation. It has been established, however, that in all vertebrates the release of mature germ cells (male and female) is dependent upon a pituitary hormone. Most of the experimental work points to the luteinizing hormone (LH) as being the

specific gonadotrophin concerned with this phenomenon. Among fish culturists, it is well known that in captivity many species will not spawn or cannot be stripped. Injection of pituitary extracts induces both ovulation and spermiation and this technique has been widely applied on a commercial scale (Atz and Pickford, 1959).

The fish pituitary normally contains a uniformly high amount of LH, except during the post-spawning period, when it is reduced for several months (Atz, 1957). A similar situation in amphibians prompted Witschi and Chang (1959) to state that the basic problem is not the quantity of LH in the pituitary, but rather the mechanism by which this and other hormones are released from the gland.

On the basis of these considerations, I suggest that spermiation in the brook trout is delayed by long photoperiods simply because this light condition does not stimulate the release of a sufficient quantity of the luteinizing hormone. Since short photoperiods do not retard spermiation, it may be assumed that such photoperiods provide the necessary stimulus for secretion of the hormone.

It is possible that a delay in functional maturity in male brook trout has a straightforward endocrinological explanation, but the retardation of the female reproductive cycle under various experimental conditions is more complicated, involving as it does both the time of initiation and the rate of gametogenesis. It does not seem useful to attempt to interpret these results in terms of specific endocrine mechanisms.

Within recent years a large number of data have accumulated from work on avian and mammalian material which show that the secretion of the gonadotrophic hormones by the pituitary is partly or wholly dependent upon, and regulated by, the hypothalamus (Harris, 1955). Donovan and Harris (1955) suggest that environmental factors exert their effects "by means of nervous reflexes originating in the wide variety of sensory end-organs" which "would appear to be co-ordinated and integrated in the hypothalamus". These workers have obtained a good deal of evidence to show that the neurosecretory cells of the hypothalamus liberate a humoral agent(s) and that this agent passes to the pituitary and regulates the secretion of gonadotrophins.

It has been demonstrated in the present study that an accelerated light regime can hasten the time of gonadal maturity in 2-, 3- or 4-year-old brook trout that are in their second or third reproductive cycles, but not in the first reproductive cycle.

The work of Foa and of Harris and Jacobsohn suggests a possible explanation of the fact that only mature brook trout are affected by an accelerated light regime. Foa (cited by Harris, 1955) showed that ovaries taken from immature animals (presumably mammals) and transplanted into adults may proceed at once to develop normally, and hence exhibit precocious function. Conversely, ovaries taken from mature or adult animals and transplanted into immature animals regress and become quiescent. Harris and Jacobsohn (1952) have demonstrated that pituitary glands, taken from rats a few days old, can maintain oestrus cycles when grafted under the pituitary stalks of hypophysectomized

adult female rats. Thus, in mammals at least, the ovaries are capable of developing prior to puberty, and at the same time the pituitary contains or can manufacture a sufficient quantity of gonadotrophins to support reproductive activity, yet the animals are not mature. Harris (1955) suggests that before puberty "there appears to be a lack of some stimulus otherwise transmitted from the hypothalamus to the adenohypophysis". The significance of these results is aptly summed up by Scharrer (1959, p. 244): "... onset of puberty is determined by the maturation of the hypothalamic mechanism rather than by the intrinsic maturation of the hypophysis, the gonads, or the reproductive tract".

It is probable that a hypothalamo-pituitary relation exists in fish similar to that which has been demonstrated in birds and mammals (Atz, 1957). If sexual maturity is determined by the maturation of the hypothalamic regulating mechanism, there is a possible explanation for the different gonadal responses observed in immature and mature brook trout exposed to an accelerated light regime. In immature brook trout, if the hypothalamic mechanism has not matured, that is has not become operative, a light stimulus could not affect the rate of release of the pituitary gonadotrophins and therefore, could not influence the rate of gametogenesis. In mature trout, however, presumably the hypothalamic mechanism has come into effect, and a light stimulus could induce an increased rate of secretion of gonadotrophins, and consequently, could bring about nearly gonadal maturity.

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Extent of Atresia in Maturing Ovaries of the Eastern Brook Trout, *Salvelinus fontinalis* (Mitchill)[1,2]

By Nancy E. Henderson[3]

ABSTRACT

Counts were made of the number of developing ova during the secondary growth phase of the oogenetic cycle in several groups of brook trout. An adjustment was made for the growth of the females since they increase appreciably in length during the secondary growth phase of the ova. Fecundity counts were then corrected to fish of a mean adjusted length. The results indicate that there is no major reduction in the number of developing ova during the secondary growth phase.

INTRODUCTION

It is commonly stated that, in all vertebrates, many of the developing ovarian follicles undergo what is variously termed atresia, resorption, or degeneration. Atresia may begin at any stage of development of the follicle and results in a reduction of the number of maturing ova. Although the corpora atretica of fish have attracted much interest, little attention has been directed to the actual number of ova that begin development compared with the number that ultimately complete oogenesis and become mature viable gametes. Recognizing the possibility of atresia in fish, various workers (e.g. Vladykov, 1956) have come to distinguish between relative and total fecundity. *Relative fecundity* refers to the number of maturing ova contained in the ovaries at any given stage of the secondary growth phase of the ova[4]. *Total fecundity* refers to the number of mature or fully developed ova produced.

In trout, as in fish generally, the number of ova is related to the size of the fish. Vladykov (1956) gave evidence which he interpreted as showing that the relative fecundity of wild brook trout is considerably higher than the total fecundity. He compared the number of maturing eggs over different ranges of ova diameter for fish that were grouped into small class intervals with respect to length. Examination of the data within each of the size classes of fish supported his thesis that the number of maturing ova decreased markedly during the process of maturation. Vladykov (1956, p. 832) concluded, "we can quite safely consider that only 56–61% of maturing eggs eventually ripen".

Normally, the number of maturing ova is established early in the secondary growth phase of the ova, and if no atresia occurs, the number will remain constant until the ova are shed. In the brook trout the size of the parent fish increases appreciably during the interval of the secondary growth phase of the ova which

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[2]Contribution from the Ontario Fisheries Research Laboratory, which is operated jointly by the University of Toronto and the Ontario Department of Lands and Forests.
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[4]The secondary growth phase is the period of rapid growth and vitellogenesis in which the ova of trout increase in diameter from approximately 1 mm to about 4 mm.

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normally takes 3.5 months to complete. Hence, as the ovarian cycle advances, there will be a progressive decline in the average number of ova present in females of a given size. This variation can be eliminated statistically by making an adjustment for the growth of the female that takes place between the time of initiation of the secondary growth phase of the ova and the time of functional maturity, based on information obtained by Henderson (1963).

MATERIAL

In the course of work on the relation of day length and temperature to gonadal development, measurements of ova size, fecundity and maternal length were obtained for various series of fish during the secondary growth phase of the oogenetic cycle. The material available consisted of 3 stocks of hatchery-reared brook trout which were used in 3 series of experiments described earlier (Henderson, 1963). Series 1 includes Experiments 1–6 of that paper, Series 2 is Experiments 7–12, and Series 3 is Experiments 14–16 (controls included).

Figure 1 is a typical graph displaying the normal oogenetic cycle. The secondary growth phase begins in early July and is completed in mid October,

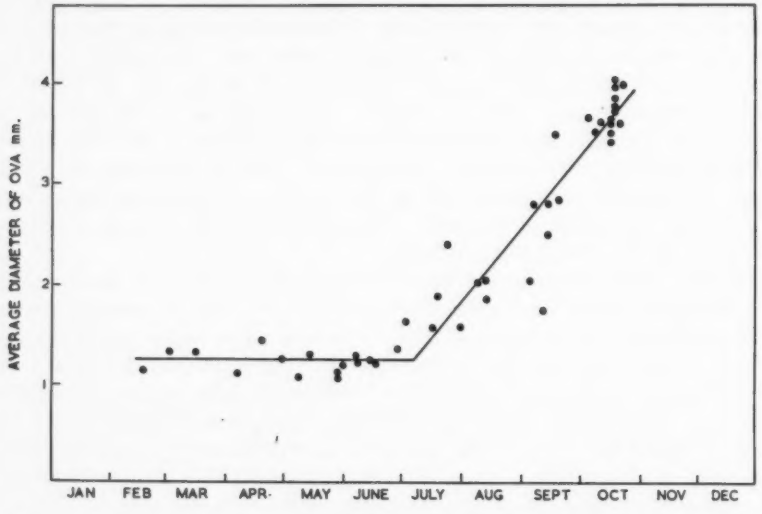

FIG. 1. Normal growth rate of the ova (data from controls to experiments reported elsewhere). Each point represents the developmental stage of one fish.

the usual time of spawning for brook trout at the latitude of Toronto. In this phase, the ova increase in diameter from 1 mm to more than 3.5 mm. (The average diameter of the ova was calculated from measurements of a random sample of 30 ova.) Also, during this 3.5-month period, the female trout may increase several centimetres in length (Fig. 2). The trend line has been calculated by dividing the data obtained during the secondary growth phase into thirds.

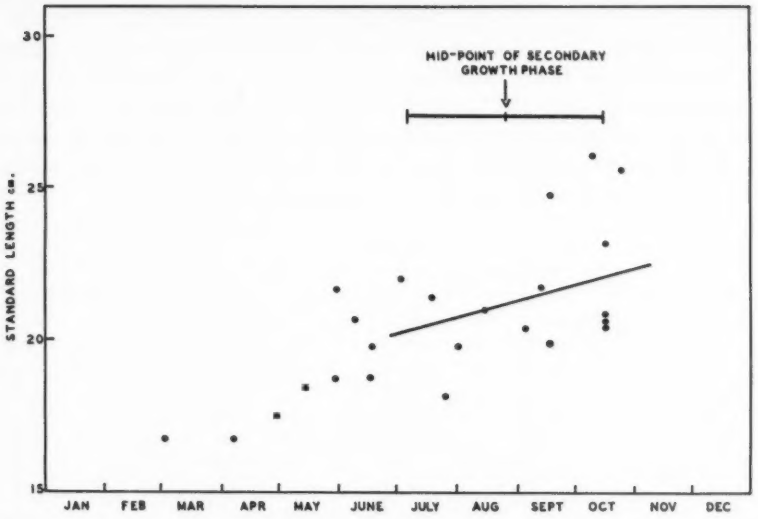

FIG. 2. Growth rate of females in a control group of fish. A *bar* has been drawn showing the temporal extent of the secondary growth phase of the ova, and an *arrow* indicates the mid-point of this stage. The line is fitted to points lying within the secondary growth phase only, by the method described in the text.

Averages were taken of the first and last thirds ($\bar{x}_1$, $\bar{y}_1$ and $\bar{x}_3$, $\bar{y}_3$) plus the average of all the observations ($\bar{x}$, $\bar{y}$). The slope was determined by joining the means $\bar{x}_1$, $\bar{y}_1$ and $\bar{x}_3$, $\bar{y}_3$. The line was then drawn through the point of means from the total data, $\bar{x}$, $\bar{y}$ (Bartlett, 1949).

Once the secondary growth phase had begun, as determined from the diameters of the ova, fecundity measurements were made. Each ovary was teased apart and the number of maturing ova determined by actual count.[5] If a female was ripe, care was taken to free any ova that were retained within the ovarian lamellae and to add these to the number found in the coelom. The number of atretic ova, larger than 1 mm in diameter, was also recorded.

Over a wide range of length (15 or 20 cm), the relation between the number of mature ova and length of fish has been shown to be curvilinear in the brook trout by Ricker (1932), Vladykov and Legendre (1940) and Cooper (1953). Rounsefell (1957) has shown that the data presented by these authors approximate a straight line when the logarithm of the number of ova is plotted against the logarithm of the length of the fish. The same transformation has been used here.

The fish used in each of the 3 series of experiments originated from different stocks of trout. Any comparison involving fecundity must initially be confined to fish belonging to the same population, since genetic differences may exist among populations.

[5]When two year-classes of maturing ova were present in an ovary, as occurred in Experiments 8 and 10, both classes were included in the fecundity count.

RESULTS

Trend lines relating age and length were calculated by the method described above for each of the 15 groups of females belonging to the 3 populations of fish. Having obtained the slopes of the growth lines, the length of each of the females in each group was adjusted to the computed size for fish of its age, at the mid-point of the secondary growth phase of the ova.[6] Averages of the adjusted lengths of the fish and of the number of ova are given in Table I.

TABLE I.

Experiment No.	Average adjusted length of fish	Average number of ova
	cm	
1	21.9	738
2	21.1	667
3	21.7	761
4	21.3	706
5	21.2	720
6 (controls)	21.3	722
7	23.4	897
8	24.3	1080
9	22.5	869
10	27.5	1340
11	25.0	1261
12	25.3	1166
14	28.6	2410
15	29.8	2298
16 (controls)	29.5	2345

The graphs in Fig. 3–5 illustrate the relation between the logarithm of the number of ova and the logarithm of the adjusted lengths of the fish in each of the 3 stocks. The trend lines have been calculated by dividing the data (as logarithms) into thirds. The grand averages for each population are shown on the graphs of the respective figures. Within each of the 3 stocks the fecundity to length relation is essentially the same, as is indicated by the similarity of the slopes of the lines and by the position of the grand mean.

In order to determine whether a significant reduction of the number of maturing ova occurs during the secondary growth phase, a comparison was made of the number of ova contained in the fish at different growth stages as indicated by the mean egg diameters. Using the trend lines in Fig. 3–5, the fecundity of each fish was corrected to the mean adjusted length of its series. Figure 6 shows a frequency distribution of the corrected fecundities arranged according to the diameter of the ova. The mean adjusted fecundities are given in Table II.

[6]Properly speaking, the correction should have been made to the size of the fish at the initiation of the secondary growth phase of the ova. However, the mid point was chosen since the data were then less radically altered by extrapolation.

TABLE II.

Diameter of ova	Average number of ova		
	Series 1	Series 2	Series 3
1–2 mm	721	927	2127
2–3 mm	730	1082	2639
3–4+ mm	714	1136	2311

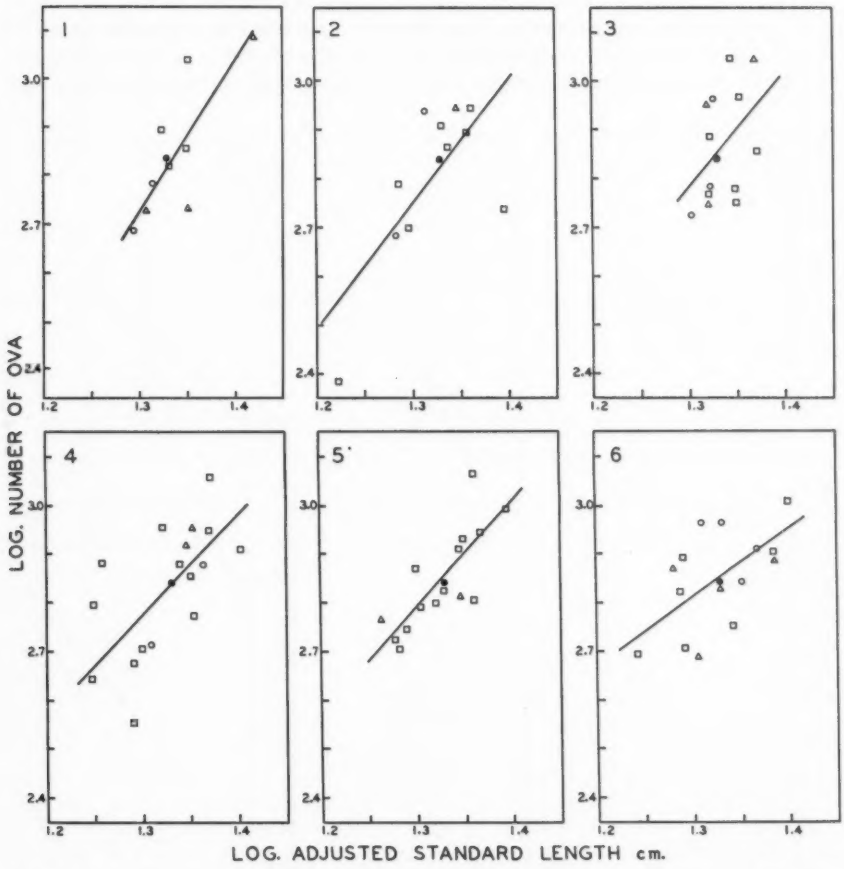

FIG. 3. Relation between logarithm of number of ova and logarithm of adjusted length, in females from Experiments 1–6. The number on each panel refers to the corresponding experiment number. The three symbols represent the average diameters of the ova — *circles:* 1–2 mm; *triangles:* 2–3 mm; *squares:* 3–4+ mm. The grand mean of all the data from this series is shown on each panel.

There is a slight increase in the number of ova in the 2–3-mm class over the 1–2-mm class, undoubtedly because some of the fecundity counts were made very early in the secondary growth phase, before the full complement of maturing ova had commenced this phase of development. From the 2–3 mm to the 3–4+ mm class there is no significant change in number of eggs in any of the 3 series, though in series 3 the mean decreases by about 10%.

DISCUSSION

Although the analysis does not indicate a significant decrease in fecundity during maturation, a small number of atretic ova are usually seen in any ovary. The average number of atretic ova observed, expressed as a percentage of the maturing plus atretic ova, varied from 3.1 to 4.7% in the three series (Experiments 8 and 10 not included (Henderson, 1963)). While a small reduction of the matur-

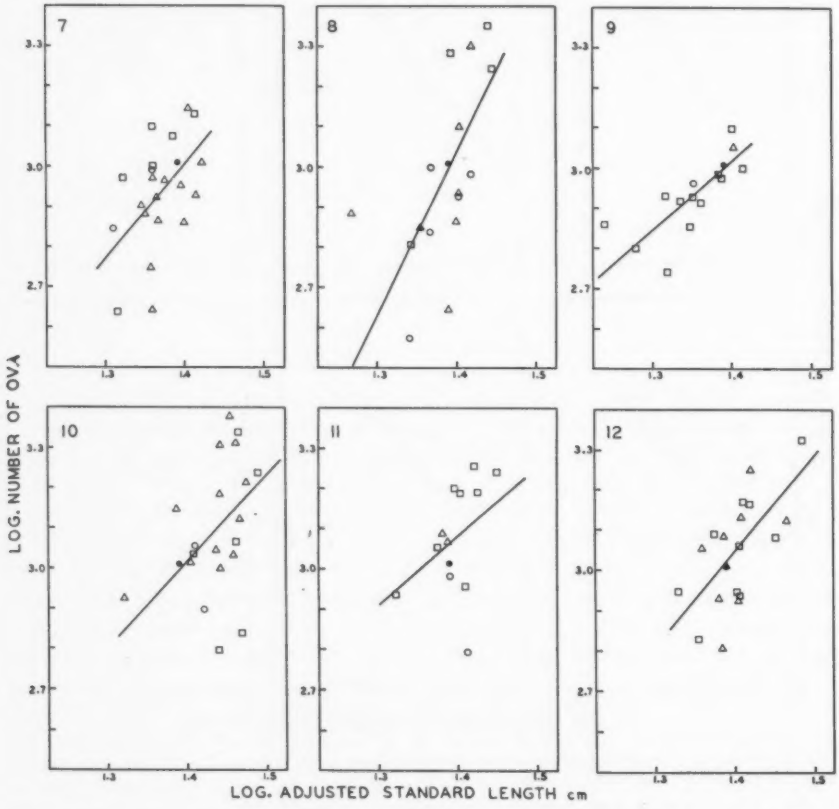

FIG. 4. Relation between logarithm of number of ova and logarithm of adjusted length, in females from Experiments 7–12. Symbols as in Fig. 3.

ing class must occur, it is not apparent in Fig. 6 partly because the values given for the 1–2-mm class are probably below the true values, and partly because of the variation in the number of ova in each of the diameter classes.

Although a slight reduction in fecundity does occur, it is by no means as large as that suggested by Vladykov (1956). His results have been misinterpreted through failure to take into account the increase in length of the female during the secondary growth phase. The growth rates of the stocks Vladykov (1956, p. 801) investigated indicate that the fish examined increased appreciably in size during this period.

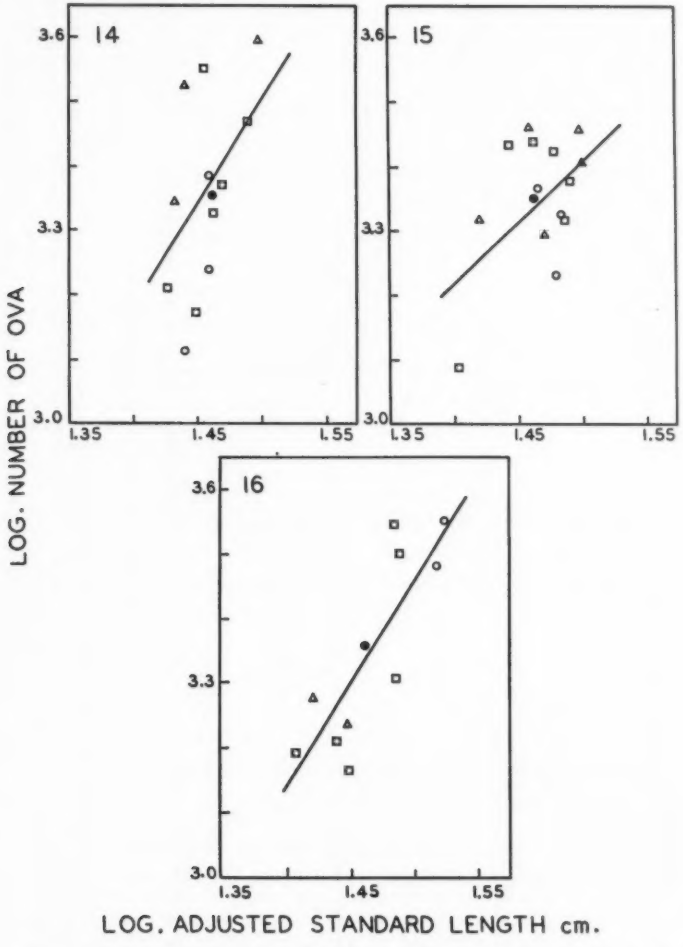

FIG. 5. Relation between logarithm of number of ova and logarithm of adjusted length, in females from Experiments 14–16. Symbols as in Fig. 3.

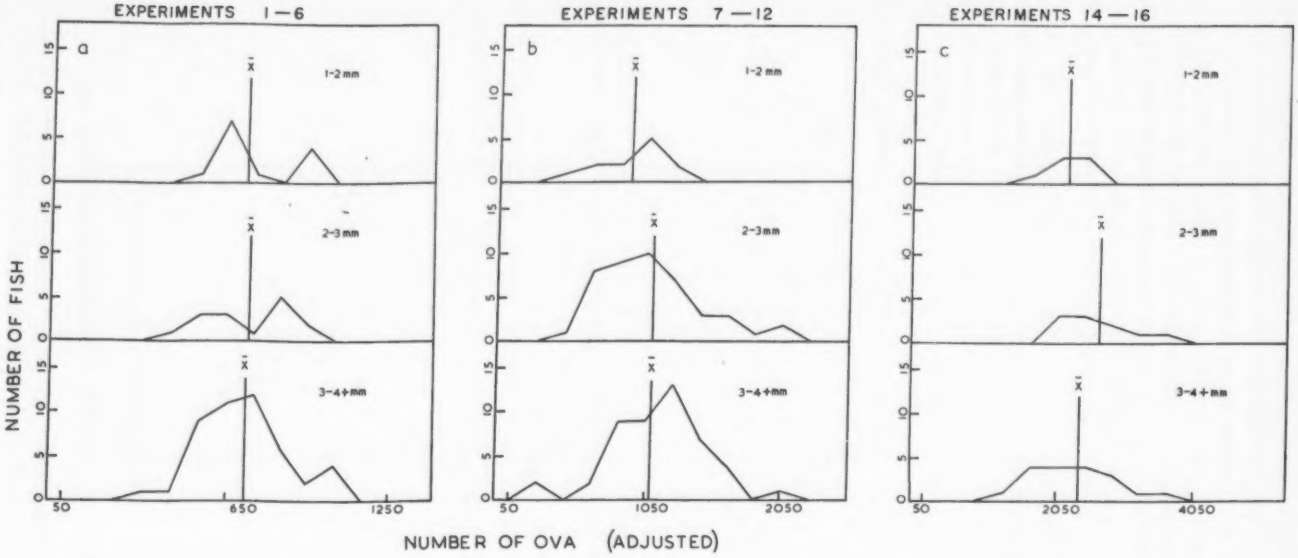

FIG. 6. Frequency polygons of the number of maturing ova, arranged according to the average diameter of the ova. The number of ova has been corrected to the mean adjusted length of the fish in the respective populations. Data from fish within each population (i.e., series of experiments) have been combined. The average computed lengths were as follows: Experiments 1–6, 21.4 cm; Experiments 7–12, 24.8 cm; Experiments 14–16, 29.2 cm. (Note that a different abscissal scale is used in each panel.)

The regression lines relating fecundity and length from all of the 15 groups of fish are shown in Fig. 7 together with the grand means from each of the 3 populations of trout. It seems likely that the relation of fecundity to length is similar within the first two series of experiments (Experiments 1–6, 7–12) and this has been indicated in the graph by a broken line joining the means from both popula-

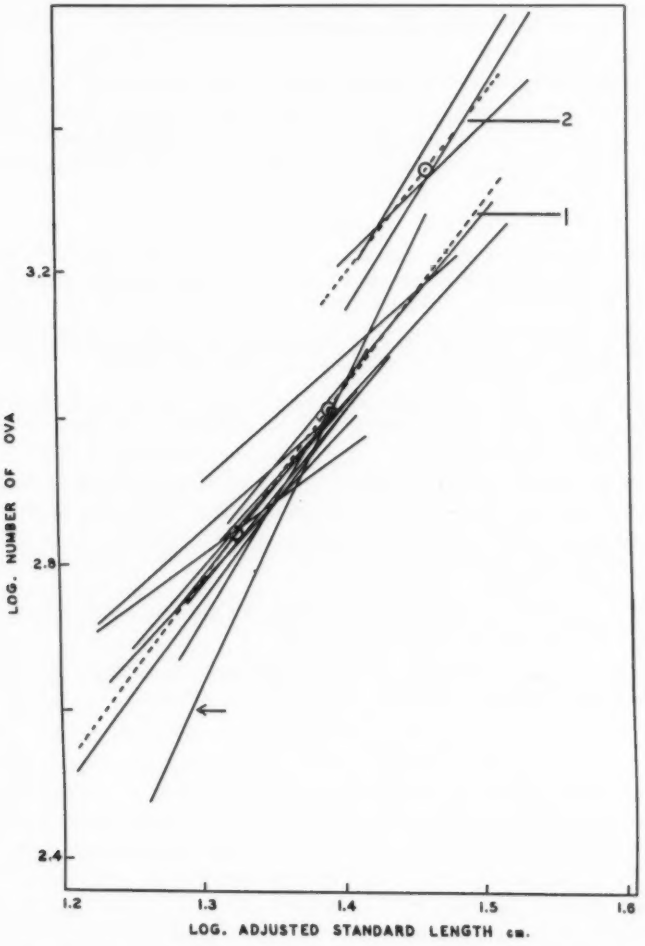

FIG. 7. Trend lines relating logarithm of number of ova and logarithm of adjusted length of females, from the three series of experiments. Solid lines represent the trend in individual experiments. The broken line marked 1 joins the mean values (open circles) of the first and second series of experiments (Experiments 1–6, 7–12); the broken line marked 2 is the approximate combined relation within the third series (Experiments 14–16).

tions. (A possible exception is the relation found in Experiment 8, which is marked by an arrow on the graph, and for which no explanation can be offered). It is possible that the relation of fecundity to length in the third population of trout (Experiments 14–16) differs from the other two stocks. A second broken line has been drawn to show the approximate relation for these fish.

ACKNOWLEDGMENTS

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Extractives of Fish Muscle. 3. Amounts, Sectional Distribution, and Variations of Fat, Water-solubles, Protein and Moisture in Cod (*Gadus morhua* L.) Fillets[1]

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ABSTRACT

The amounts, sectional distribution and some variations of fat, water-solubles, protein and water in cod fillets have been determined on defined, pre-rigor samples. It was found that the head-end of the fillet is the richest in protein. The middle section is the richest in water-solubles while the tail-end contains more fat and more water than any other part of the fillet. Only slight differences in the major components were detected between male and female specimens.

INTRODUCTION

The importance of physiological factors on the biochemical composition of salmon and herring has been stressed by the studies of Idler, MacLeod and Tarr, and were recently reviewed by Tarr (1959).

The scarcity of reliable data on chemical composition of fish has been pointed out by Stansby (1947), Love (1957) and Love *et al.* (1959). The latter work is the first attempt to extract from the huge number of publications dealing with the chemical composition of fish the data that could be reliably used for further work. The main touchstone used in that paper was the adequacy of sampling. Biochemical analysis generally is accomplished in four steps: sampling, extraction, fractionation of the extract and identification or measurements of the isolated components. With the advent of the various types of chromatography and spectroscopy and the automation of many analytical procedures, the two last steps nowadays can be performed with satisfactory accuracy and speed. The extraction techniques still rest mostly on empirical foundations and to obtain significant and reproducible results, the operator must adhere strictly to the prescribed conditions. The sampling as a rule is fortuitous and as yet lacking either theoretical or empirical foundations. The chemical composition of fish varies in wide limits according to its age, size, stage of sexual maturity, diet and other factors. The effect and the significance of some of these factors have been reviewed recently by Love (1957) and Jacquot (1961). Which of these factors is predominant and which can be disregarded in sampling is not yet known. The purpose of this paper is to report some results of an exploratory study on the amounts, distribution and variations of the main components of the edible part

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of cod. It is hoped that these results may lead to a more rational choice and preparation of the analytical samples of cod tissue. A report of the observations in seasonal variations of the chemical composition of cod muscle is in preparation.

EXPERIMENTAL

Origin of Fish

From tagging experiments and vertebral counts it appears that the cod populations inhabiting the inshore waters of Nova Scotia are largely stationary with only slight mixing between neighbouring inshore or offshore populations (McKenzie, 1956). The degree of homogeneity of these populations is such that the cod of any one inshore area in this region can be distinguished from those of adjacent areas on a basis of vertebral counts (McKenzie and Smith, 1955).

A fishing community, Terrence Bay, centrally located in one of such areas twenty miles south of Halifax was chosen as a permanent source of cod for this series of experiments. This area is also known as sector XXI-M on the map of the North Atlantic Council of Fishery Investigations.

The fish were caught by hand lines, put into a portable cooled sea water box and transported without delay by truck to the laboratory in Halifax.

Sex and Size of Fish

The usual commercial classification of cod along the Nova Scotian shore is "scrod" under $2\frac{1}{2}$ lb, "market cod" from $2\frac{1}{2}$ to 10 lb, and "steak" over 10 lb (McKenzie and Smith, 1955). The weight–length relationship for cod of the southern part of the North Atlantic is given in tables of Bigelow and Shroeder (1953). Consequently the length of "scrod" is 20 inches (51 cm) and below; the length of "market cod" is 20 to 30 inches (51–76 cm), and cod over 30 inches is classified as "steak".

British workers have accumulated a certain amount of data on the macrochemical variations in the tissue of North Sea cod. Of particular interest are the variations due to the size of the specimen. Love (1960) showed that the water content and the variations in the hydration of the tissue over a 1-year period were different in specimens of small, medium and large size. Olley *et al.* (1962) found that the tissue of scrod-class cod contains 0.804% lipid, the market-class has 0.667% and the tissue of the steak-class cod with 0.630% fat is the leanest. The seasonal variations of lipids in the tissue of North Sea cod were lacking (Olley *et al.*, 1962; Olley and Lovern, 1960), or if existing, they would affect the true fat (triglycerides) only (Lovern *et al.*, 1959).

It is also of interest to note that the amplitude of variations in fat content over a 1-year period in Canadian Atlantic herring (*Clupea harengus*) in mature stage is from 4.1 to 17.4% (Leim, 1957) while the amplitude of fatness in immature, sardine-size herring is considerably wider, from 1.2 to 27.5% (Leim, 1958).

The results of preliminary extractions, which are not reported here because seldom were all the components determined on the same sample, indicated that the individual variations of the macrochemical composition in the tissue of the scrod-class cod were more pronounced and more erratic than in the specimens of market-class cod.

The macrochemical composition of female and male cod did not differ markedly within the market class when the fish were caught simultaneously and on the same fishing ground. For these reasons it was decided to avoid the use of cod from the scrod class, keeping the size limits between 22 and 24 inches (56–61 cm) and not to discriminate between male and female fish. This latter decision was justified in a later stage of experiments when an opportunity occurred to extract separately larger batches of the same size female and male cod caught simultaneously on the same fishing ground. These results are shown in Table I. The size and age of cod at maturity in this particular region of the Atlantic has

TABLE I. Macrochemical composition of fillets taken from male and female cod (23 ±1 inches long) three months after spawning.

	Number of fish used	Percent wet weight of muscle			
		Fat	Water-solubles	Protein	Water
Male cod	5	0.98	2.73	16.04	80.25
Female cod	11	1.02	2.62	15.76	80.62

not yet been definitely determined. It can be roughly interpolated from the data for cod of the Newfoundland area (Fleming, 1960), the measurements in the Southwestern Gulf of St. Lawrence (Powles, 1958) and the data for the Gulf of Maine (Bigelow and Schroeder, 1953). From these data it appears that the cod of Terrence Bay within 22–24 inches (56–61 cm) long should include more than 50% mature specimens. An attempt was made by unskilled personnel to grade the fish used in these experiments for maturity according to the maturity tables of Powles (1958). Over a period of thirty months the gonads of this length group were found to be mature and only a few specimens longer than 22 inches (56 cm) were discarded as obviously immature. However these determinations were made without the guidance of a competent biologist.

PREPARATION OF SAMPLE

On arrival at the laboratory, fish of suitable size were selected, killed by a blow on the head, and immediately filleted, skinned and deboned by a skilled worker. The fillets were inspected for parasites and diseases. The gonads were inspected for sex and maturity and the contents of stomachs for the amount and kind of food. Four samples from selected fillets were excised. The samples were taken from the head-ends of the fillets (H), from the middle or belly sections (B), from the tail-ends (T), and the fourth sample (C) was prepared from the remaining parts of the fillet (Fig. 1). The (C) sample served as a control for direct determination of total solids and water.

EXTRACTION

APPARATUS. A two-speed Waring Blendor with 500-ml screw-capped jars was used. To maintain the same blending conditions throughout the series the bearings and the blades were readjusted monthly.

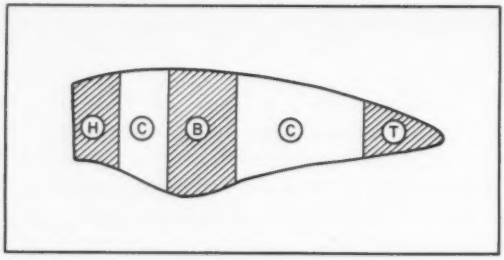

FIG. 1. Parts of the fillet from which samples were taken: H — head-end; B — belly; T — tail-end; C — parts used for control sample.

SOLVENT. A reagent grade isopropanol was used either anhydrous or with 25% added water. The amount of dry alcohol to be used in the first extraction was calculated to make with natural water of the tissue a liquid phase containing 25% water. Isopropanol with added 25% water was used in the second extraction and for the washings. Anhydrous solvent was used in the third extraction. The dilution of 25% was chosen for two reasons: first, because it is in the range where the maximum extraction of fat is achieved; and second, because the solvent-soluble proteins at this dilution are extracted only in negligible amounts (Dambergs, 1959).

THE DURATION OF EACH EXTRACTION. It was found that with blendors in proper condition there was no advantage in extending the blending period at high speed beyond 4 minutes for samples not exceeding 100 g. Longer periods increased the yields only slightly but had the disadvantage of raising the temperature of the slurry. The increase in temperature due to the blending was considered as normal when it did not exceed 10° C. The duration of each extraction was controlled automatically. A short preliminary homogenization preceding the first extraction, with gradual addition of solvent, increased the reproducibility of the results.

NUMBER OF EXTRACTIONS. The results of a typical exhaustive extraction of cod muscle at room temperature with isopropanol containing 25% water are shown in Table II. It can be seen that the first two extractions produce about 99% of the total fat and about 84% of the water-solubles extractable with this solvent. A third extraction with the same aqueous solvent would complete the extraction of fat and raise the yield of water-solubles to 93%. However for further analyses it was more important to obtain the protein in a loose fibrous or powdery form than to have a more complete extraction of the water-solubles. Furthermore, the results of such extractions are so reproducible that the true amounts of extractives can be calculated from partial extracts. For these and for time-saving reasons, the aqueous alcohol was used in only two extractions and anhydrous solvent was used for the third and last extraction.

PROCEDURE. The fillets were aligned on a tray and slices of approximately the same size were cut crosswise from the extremities and the belly region of each

TABLE II. Extractives obtained from 100 g cod muscle by repeated extractions at room temperature with isopropanol containing 25% water.

	Fat (A)		Water-solubles (C)		Crude extract (A + C)	
	mg	%	*mg*	%	*mg*	%
I Extraction	990	95.8	1830	66.0	2820	74.2
II Extraction	37	3.6	495	17.8	532	14.0
III Extraction	6	0.6	255	9.2	261	7.0
IV Extraction	0	—	110	4.0	110	2.8
V Extraction	0	—	75	2.7	75	1.9
VI Extraction	0	—	5	0.2	5	0.1
Total:	1033	100%	2770	100%	3803	100%

fillet until a sample of 100 g was prepared from each part of the fillet. Then the weight was adjusted to 100.0 g exactly and the sample placed into a blendor jar and the solvent added in three portions with a half-minute blending at low speed after each of the first two additions. Then the rest of the solvent was added and the blendor set at high speed for 4 minutes. The resulting slurry was filtered through a coarse sintered glass filter, and the jar and the filter cake were washed with about 100 ml of aqueous isopropanol. The filter cake was returned to the jar for a second 4-minute extraction at high speed with isopropanol containing 25% added water. The filtration and washings were done as before and the filter cake re-extracted for the third time with anhydrous solvent. The filtrates of each sample were combined in 1000-ml volumetric flasks. Water was added to dilute the dry alcohol used in the last extraction and the flasks filled to the mark with isopropanol containing 25% water. The filtrates were colourless and clear or only slightly opalescent. They have been kept without apparent signs of deterioration for two years.

FRACTIONATION OF THE EXTRACTS

CRUDE EXTRACT, FAT, WATER-SOLUBLES. The amount of solids in the filtrate after evaporation of the solvent is called the crude extract. It was practically free of proteinaceous materials. The weight of the precipitate obtained by adding trichloroacetic or perchloric acid to the extract was less than 1% of the crude extract. The crude extract was separated into two fractions — ethyl ether soluble fraction, called fat, and the ether-insoluble fraction, called the water-solubles.

For the determination of fat and water-solubles 100-ml aliquots of the filtrates were evaporated under vacuum to apparent dryness. The crude extract was eluted by decantation with small portions of ethyl ether. Addition of a few drops of water greatly facilitated the separation. After evaporation of the solvent and drying to constant weight the amounts of fat and water-solubles were expressed as percentages of the wet weight of the sample.

PROTEIN. The protein was determined by weighing the thoroughly dried filter cake. The corrections to be made due to the losses in the blending jar and

on the filter were determined to average only 40 mg per sample. The drying was done in a vacuum oven at 65° C. Constant weight was reached in approximately 24 hours. On two occasions the residual moisture in the protein was determined by Karl Fisher reagent. The results were 0.2 and 0.3% of moisture. No corrections for this excess of weight were made.

The unextracted control sample (C) was dried to constant weight simultaneously with the three protein residues. The average results from these control samples are shown in the bottom lines of Tables III and IV.

WATER. The water was calculated by difference between the weight of sample and the amount of solids in the sample.

RESULTS

Attempts to determine the differences in the chemical composition of cod muscle due to sex gave results indicating that such differences are small and that particular care in sampling is necessary to produce significant evidence of these differences. Five male and eleven female fish, all 23 ±1 inches long were selected from a catch of 48 cod taken simultaneously in late August. Whole fillets of each sex were minced, mixed, and samples extracted as described above. The results are shown in Table I.

These results are corrected for complete extraction at room temperature with isopropanol containing 25% water. They represent the total amount of fat and about 90% of the water-solubles present in the sample. An additional 10% of water-solubles could be extracted by the use of boiling solvent, however it is not yet known how much of this amount would come from the breakdown of protein.

According to the maturity tables of Powles (1958), all the selected fish were mature and their gonads were in the "recovering" stage. With regard to the feeding cycle of cod, August in Terrence Bay is the period of resting or normal feeding which follows the voracious post-spawning feeding period from May and June to July. The average results of twelve monthly determinations of fat, water-solubles, protein and water in various parts of cod fillets are shown in

TABLE III. Average results of twelve monthly analyses of cod fillets taken in 1960 from 36 fish 23 ±1 inches in length.

Part of fillet	Fat (A)	Water-solubles (B)	Crude extract (A + B)	Protein (C)	Total solids (A + B + C)	Water
	%	%	%	%	%	%
Head-end	0.96	2.26	3.22	16.42	19.64	80.4
Middle section	0.93	2.34	3.27	15.79	19.06	80.9
Tail-end	1.13	2.29	3.42	15.37	18.82	81.2
Whole fillet	0.99	2.31	3.30	15.84	19.14	80.9
Control sample					19.25	80.7

TABLE IV. Average results of twelve monthly analyses of cod fillets taken in 1961 from 66 fish 23 ± 1 inches in length.

Part of fillet	Fat (A)	Water-solubles (B)	Crude extract (A + B)	Protein (C)	Total solids (A + B + C)	Water
	%	%	%	%	%	%
Head-end	0.97	2.26	3.23	16.17	19.40	80.6
Middle section	0.96	2.32	3.27	15.60	18.86	81.1
Tail-end	1.17	2.30	3.47	15.25	18.72	81.3
Average for fillet	1.01	2.30	3.31	15.66	18.97	81.0
Control sample					18.96	81.0

Tables III and IV. Table III represents the results obtained in the 1960 calendar year when during the first eight months only 1 or 2 fish were analysed per month and at least 5 fish monthly were used for the rest of the year. A total of 36 fish was used in 1960. The results for 1961 (Table IV) were obtained using not less than 5 fish in each monthly sample and a total of 66 fish.

DISCUSSION

The direct isolation and gravimetric determination of the water-solubles was adopted because the results thus obtained reflect more directly the composition of the fillet and the regional and seasonal variations of these compounds rather than the abstract values of the "non-protein nitrogen". Moreover, the results thus obtained are of immediate help for the better understanding of some technological processes, e.g. the production of fish protein concentrate or fish meal. The name "water-solubles" was preferred to the traditional name for this group of components ("non-protein nitrogeneous compounds") because whatever method of extraction is used this fraction includes also such important compounds as sugars, vitamins, phosphates and mineral salts devoid of nitrogen. This group of components and their variations would pass unaccounted by the use of the non-protein nitrogen method.

The direct gravimetric determination of protein was preferred to the usual determination by total nitrogen and the subsequent use of the controversial factor of conversion. It has already been pointed out that the studies of proximate analyses of Canadian Atlantic fish pursued at this Laboratory (Fraser *et al.*, 1961), using the traditional nitrogen analyses for protein determinations, produce comparable results to those shown in Tables III and IV. The determination of nitrogen along with some other elements in the samples of purified protein, water-solubles and fat, accumulated during this series of extractions, is in progress in an attempt to detect the pattern of their regional and seasonal variation in the musculature of cod.

The comparison of the gross compositions of male and female cod tissue in Table II shows that the differences are small and could be neglected in explora-

tions of the present type. However they were observed constantly in all comparisons carried out on smaller samples during the same "resting period".

Furthermore, these results appear to be in good agreement with the findings for cod in the Baltic Sea (Kordyl, 1953). In clupeids the macrochemical variations appear to be more pronounced than in gadoids. However no significant differences between males and females were apparent in a large scale investigation of the Pacific herring (McBride *et al.*, 1959). Unfortunately no results have been collected as yet for other periods of the sexual cycle of cod.

From Tables III and IV it can be seen that fat, water-solubles, protein and water are distributed unevenly throughout the fillet.

The distribution of fat in the edible part of herring has been studied in great detail (Brandes and Dietrich, 1953) and there is a tendency to generalize the results obtained from herring to the gadoids. However, Tables III and IV show that the distribution of fat in cod muscle is just the opposite to that in herring. The highest concentration of fat is found in the tail-end of the fillet, while the belly part and the nape-end are leaner. On the year-averages the difference is about 20%. The fat values shown in the Tables are uncorrected experimental values and represent not less than 98% of the true amount present in the samples.

Similar distribution of fat has been reported for another gadoid — the stockfish or the African hake, for which the following figures are given: fat content in the nape-end of the fillet, 1.25% on dry basis; fat content in the caudal end, 4.5% (Meltzer and Spuy, 1951).

The water-solubles are distributed almost evenly throughout the whole length of the fillet. However the small variations shown in Tables III and IV which indicate that the concentration of the water-solubles in the abdominal region is slightly higher than it is in the adjacent areas was regularly observed in more than thirty monthly measurements. The same is also true for the slightly higher concentration of water-solubles in the tail-end as compared to the head-end of the fillet. These results represent only about 85% of the total water-solubles extractable at room temperature. The main difficulty in the accurate gravimetric determination of this group of components is the determination of constant weight. Reproducible results were obtained and the small differences became evident only when all extracts were dried under well controlled conditions. Among the water-soluble compounds some are highly hygroscopic, some carry water of crystallization and some can be easily destroyed by heat with a loss of volatile products. For this reason the results obtained are valid only for these conditions of extraction and drying but they are useful to detect the variation in distribution of the water-solubles and their seasonal variations.

The gravimetric determination of the two major components (protein and water) is quite adequate for the detection of the distribution in the fillet. The results obtained show that there is an appreciable and gradual decrease of the protein from the head-end to the tail-end of the fillet. The water content varies at the same rate but in the opposite direction.

The appearance of the protein depleted of its fat and water solubles was quite characteristic for the three sections of the fillet. The protein of the head-

end was white and finely fibrous. The belly section produced powdery chalk-like protein while the protein from the tail-end was darker in color, either grayish or brownish and coarsely fibrous.

No extreme variations in water content were observed and the figure 81.0% water was an average. Abnormally high hydration of the tissue was observed only with cod having more than three nematodes per fillet. As a rule the fat content in such sick specimens was below average while the amount of water-solubles was above normal. Whenever detected such fillets were discarded.

The variations in the distribution of the main compounds along the fillet are more apparent when expressed on the basis of the dry weight of the fillet.

TABLE V. Distribution of the main components in cod fillets taken in 1961, as percent of the dry weight of the sample.

	Percent dry weight of sample		
	Fat	Water-solubles	Protein
Head-end	5.0	11.70	83.4
Middle section	5.1	12.30	82.7
Tail-end	6.3	12.28	81.5
Whole fillet	5.3	12.15	82.6

CONCLUSIONS

The direct gravimetric determination of the main groups of components extracted at room temperature from cod muscle with isopropanol containing a controlled amount of water proved to be a useful tool for the macrochemical analysis of fish tissue.

The sectional distribution of fat in the Canadian Atlantic cod does not follow the pattern of the distribution of fat in herring. The regional variations of fat, water-solubles, protein and water in cod fillets are important enough not to be neglected in the preparation of samples for any biochemical analysis. Differences in the composition due to the sex exist but their magnitude was determined only for the "resting period" when possibly these differences were at their minimum. The use of the same length of fish for comparative studies is very important and more detailed investigation of the age factor in the macrochemical variations in cod muscle would be beneficial.

ACKNOWLEDGMENTS

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Observations on the Migration of Young Sockeye Salmon (*Oncorhynchus nerka*) through a Large, Complex Lake System[1,2]

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ABSTRACT

The seaward migration of sockeye salmon smolts through the Babine Lake system to its outlet is examined by extensive tagging, direct observations and experimental orientation tests. The migration appears to be a well-oriented, non-random movement; it apparently commences from all lake regions at about the same time, suggesting a common triggering stimulus. When migrating, the smolts swim at a speed of 0.65 to 1.0 feet per second. The migration appears to take place primarily at near-surface depths; diurnally, most of the migration activity appears centered around the evening dusk period. There is a consistent increase in rate of travel as the season progresses; in large part this appears a result of increasing migration drive. Orientation tests with a view of only the sky show the smolts capable of time-compensated orientation in relation to celestial phenomena, and such tests at various points along the migration route show the preferred direction of smolts to correspond with the direction of most direct route to the outlet. Most smolts of the system show a constant preference for the northwesterly direction which would lead them rather directly to the outlet. However, one group which in the course of its migration to the outlet must make a 180° turn clockwise from southeast to northwest is found to have a corresponding shift in directional preference with time. Simple one-direction orientation, in one case shifting with time, is sufficient to account for ability to find the outlet. A positive relation is shown between rate of travel of tagged smolts and the hours of sunshine on days subsequent to their release.

INTRODUCTION

The sockeye salmon (*Oncorhynchus nerka*) is an anadromous species in which the young typically remain in lakes for one year (sometimes longer) before migrating seaward. This paper concerns itself with an examination of the seaward migration of young sockeye salmon through the Babine Lake system in north-central British Columbia (Fig. 1).

During the August–October period each year, sockeye salmon spawn in the outlet of Babine River (above and below Nilkitkwa Lake) and in the various tributary rivers shown. The following May and June the resulting progeny emerge from the gravel as free-swimming fry and enter the lake where they take up a pelagic, zooplankton-eating existence; one year later, in May and June, nearly all emigrate seaward. Thus, each year there is an exodus from the lake of yearling sockeye, known at this stage of their life as smolts.

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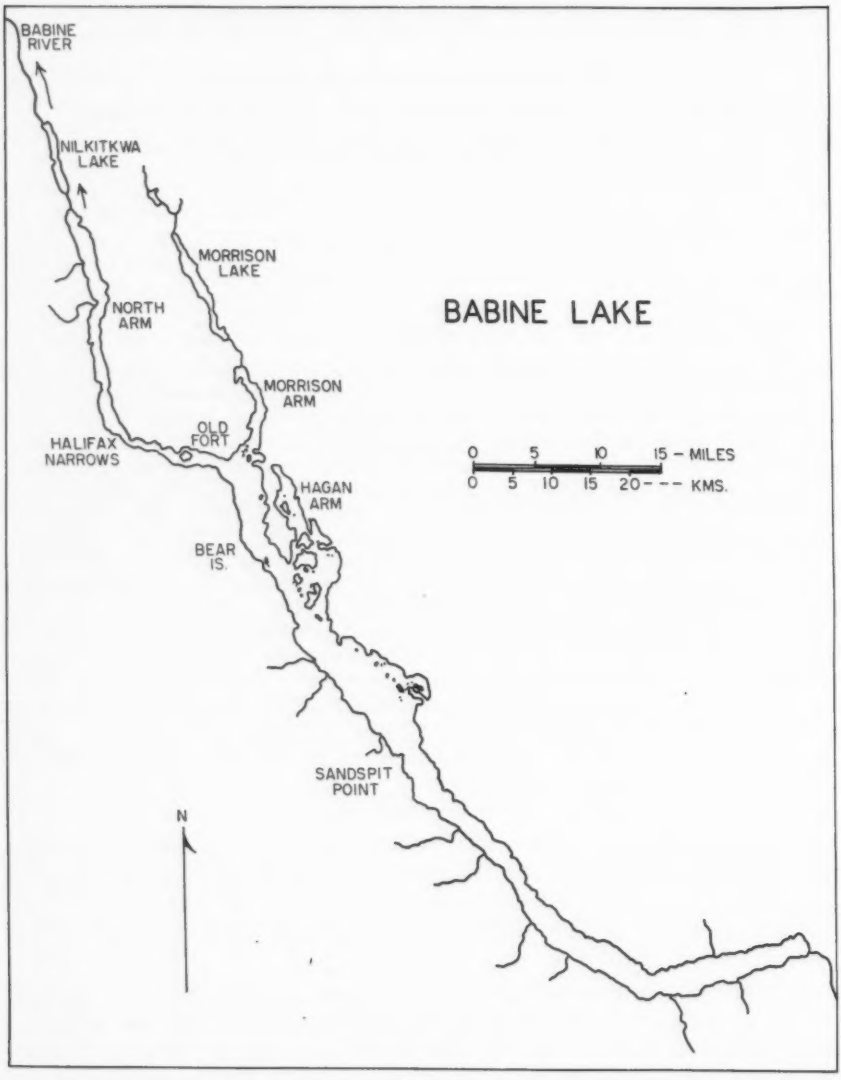

FIG. 1. Map of the Babine Lake system showing the tributary spawning grounds of sockeye salmon.

During their year of lake life the young sockeye of the multibasin Babine system have been found to have a most non-uniform distribution, owing to limited dispersal from their points of entrance as fry. There is apparently an initial dispersal of fry from the various spawning grounds resulting in rather distinct populations becoming associated with the more or less distinct basins.

These populations vary greatly in density and, as a result, in growth rate of the individuals. Populations of greatest density (and with individuals of slowest growth rate) are consistently found in the small lake basins of Nilkitkwa Lake and the North Arm of Babine Lake, which receive the fry from the heavily used outlet spawning grounds (Johnson, 1956, 1958, 1961).

Figure 2, illustrating the distribution of young sockeye during the summer and autumn of 1959, is typical. There is shown: (1) a localization of very dense

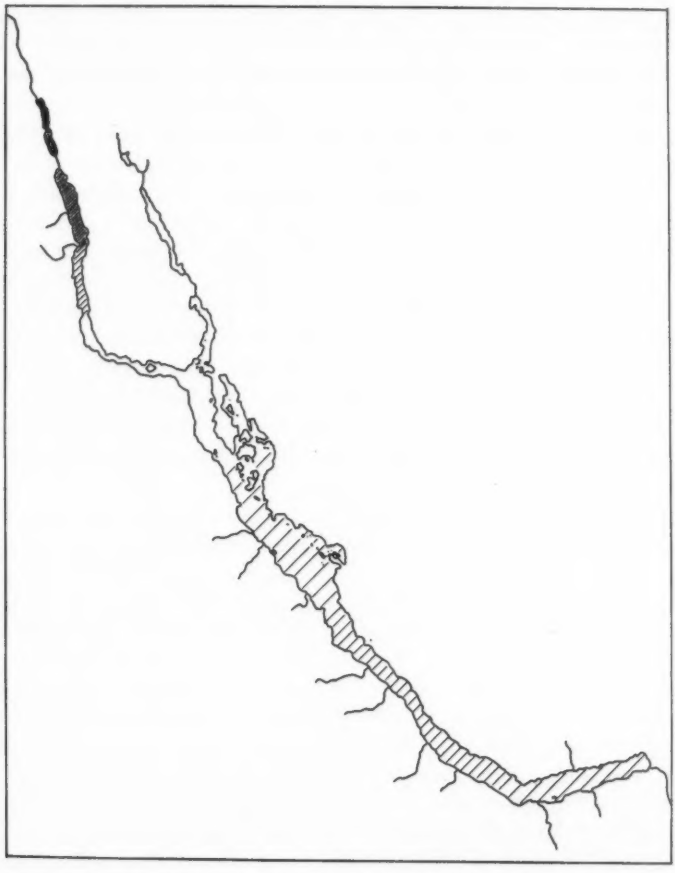

FIG. 2. The distribution of young sockeye salmon in the Babine system during the summer and autumn of 1959, shown diagrammatically with degree of shading proportional to population density.

populations in the basins nearest the outlet region; (2) a further uplake zone (including the south basin of the North Arm, Morrison Arm, the Old Fort to Bear Island basin and Hagan Arm) with only one small spawning tributary and extremely sparse populations of young sockeye; and (3) the large, furthest uplake

basins with populations of only moderate density, but because of their size containing a great number. (No direct evidence of density of the Morrison Lake population is available, but based on the number of spawning sockeye on its tributary spawning grounds and the size of the smolts migrating from it, it is believed to be moderate.) Sampling in the spring just prior to the smolt migration indicates that this bimodal (with respect to distance from the outlet) distribution essentially maintains itself over winter and up to migration time.

The purpose of this communication is to make a general description of the migration through the lake to the outlet and to present a theory which adequately accounts for it.

Investigation of this migration has involved, primarily, the use of three techniques:

(1) *Direct observation of near-surface migration activity.* Throughout its lake life the sockeye salmon is a schooling species, schools varying in size from several hundred to several thousand individuals. A characteristic form and behaviour, involving a great deal of nipping of the surface, make these schools evident and readily identifiable when near the surface. In calm weather, actively migrating schools can be observed near the surface. Their direction, speed and horizontal distribution have been determined by observing from boats and from high observation points along the lake using field glasses and a surveyor's transit.

(2) *Tagging.* Periodically during the migration smolts were captured, tagged and released at three different uplake locations. Tags of a different colour, or colour combination, were used for each tag release. Trapping of migrating smolts at the outlet and at the three uplake tagging sites throughout the run allowed for recovery of tagged fish.

(3) *Tests of the orientation of smolts when their vision was restricted to the sky.* The apparatus and technique used was similar in principle to that developed by Kramer (1950) and extensively used for testing orientation of birds. These tests were carried out on single fish in plastic-bottomed tanks with shielded walls high enough so as to permit vision of the sky only. The height of the sidewalls was always such that the view of the sky from the centre of the tank was 90°. The observer was lying underneath the tank on a curtained platform where he could observe the fish against the sky from this darkened chamber. After some preliminary observations over 24-hour periods, tests later on were restricted between noon and midnight, at 3- to 5-hour intervals. In this paper only the tests done at noon, mid-afternoon, and the dusk period were used. The observation periods were 15 or 30 minutes in 1960 and 15 minutes in 1961. Directional preferences of the smolts were here based on the direction in which the fish was pointing when standing still. A system of scoring was used whereby every time the fish was pointing in a certain compass direction for 3 to 5 seconds one score was recorded for that direction. In construction of the circle diagrams the compass direction with the highest score was taken as 100% (is the distance from centre to the circumference of the circle) and the scores for the other directions calculated relative to this one. Tanks and position of observer were rotated after every test to eliminate possible cueing on the tank itself. Tests were done,

as far as possible, only with smolts that were actively migrating at the time of capture, and the holding tanks were situated in such a way that normal light-dark cycles existed.

Additional sources of information have been (a) an independent program of daily mark and recapture to estimate the number of smolts leaving the system, which is carried out at the outlet throughout the run, and (b) fishing with standard nets throughout the lake system prior to and during the migration.

EVIDENCE OF THE GENERAL PATTERN OF MIGRATION TO THE OUTLET

Figure 3 shows the location of the uplake tagging sites and the outlet recovery site; it also lists the total number of smolts tagged at each site and the number of such tagged fish subsequently recovered. In 1960, fish were tagged at the Halifax Narrows site only. In 1961, smolt trapping at three uplake sites permit-

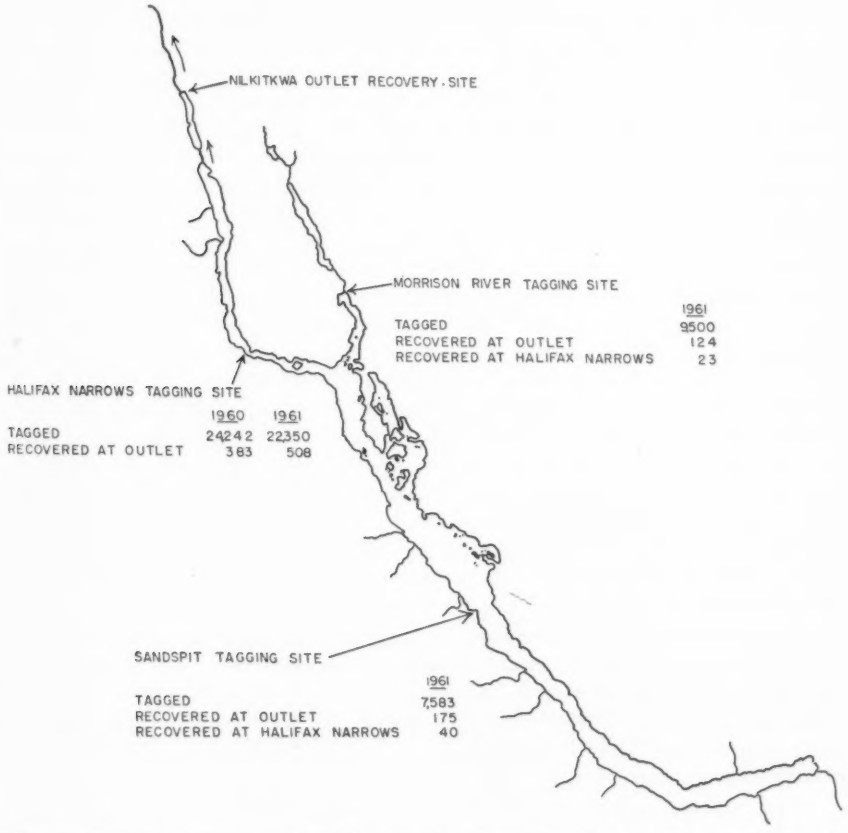

FIG. 3. Tagging and recovery sites, 1960 and 1961. Shows number of smolts captured, tagged and released at each tagging site and the number and location of those subsequently recaptured.

ted recovery of tagged fish other than at the outlet: 23 of the smolts tagged at Morrison River and 40 of the smolts tagged at Sandspit were recaptured at the Halifax Narrows site. No recaptures of tagged smolts from other tag release sites were made at either the Morrison or Sandspit sites. This indicates well-oriented, non-random movement in the direction of the lake outlet. Also indicative of non-randomness and good orientation is the fact that wherever near-surface migrating schools were observed they were seen moving in the direction of the most direct lake route to the outlet: the few exceptions to this were usually moving in the diametrically opposite direction. "Reversed orientation" under experimental conditions will be noted in the discussion of orientation tests below.

Figure 4 shows the rate of travel of tagged fish from their points of release to the outlet. Rate of travel from the three tagging sites to the outlet is expressed as the average number of miles per day covered on the most direct route (from Halifax Narrows, 27 miles; from Morrison River, 46 miles; and from Sandspit, 63 miles) in the time between release and recapture. That is, it is merely the number of miles by the most direct route to the outlet divided by the mean number of days between release and recapture. All releases and recaptures were made at the same time of day — during the evening twilight and early dark period when the diurnal peak of migration activity occurs. In all cases an increase in rate of travel as the season progressed was noted. The rate of increase was very similar for all three cases examined in Fig. 4A–C, as evidenced by the regression coefficients. Part of this increased rate of travel might be expected as a result of the effects of rising temperatures on swimming speed. Based on the data of Brett *et al.* (1958) the proportional increase in speed that would be expected as a consequence of the rise in lake temperatures from about 7 to 13° C is shown in Fig. 4D. Another source of increase (no doubt less than indicated in Fig. 4D, which assumes a constant movement toward the outlet of only the surface 10 feet of water, and that the fish are continually in this depth range) would be due to an increasing discharge rate of the water during this time of year, effecting passive transport toward the outlet. Figure 4D shows that the effects of both these factors are insufficient to account for the observed rate of increase in migration speed. The residual, unaccounted-for increase is believed to be probably due either to a general increase in duration of migration time per day, or to an increase in speed of swimming possibly connected with a more straightforward orientation, or to a combination of these factors. We might refer to this as an increase in migration drive.

Regardless of causative factors, it is obvious that in comparing rates of travel and effects of environmental factors on rates of travel, at different times during the migration, the relationships with time as shown in Fig. 4A–C must be taken into account. Thus, in comparing different years and different tagging sites, rates of travel have been adjusted to a common date (June 1) on the basis of their regression relation with time.

The adjusted mean rate of travel from Halifax Narrows to the outlet was 3.2 miles per day in 1960 and 4.9 miles per day in 1961. This difference is significant and it will be considered below. There were no significant differences

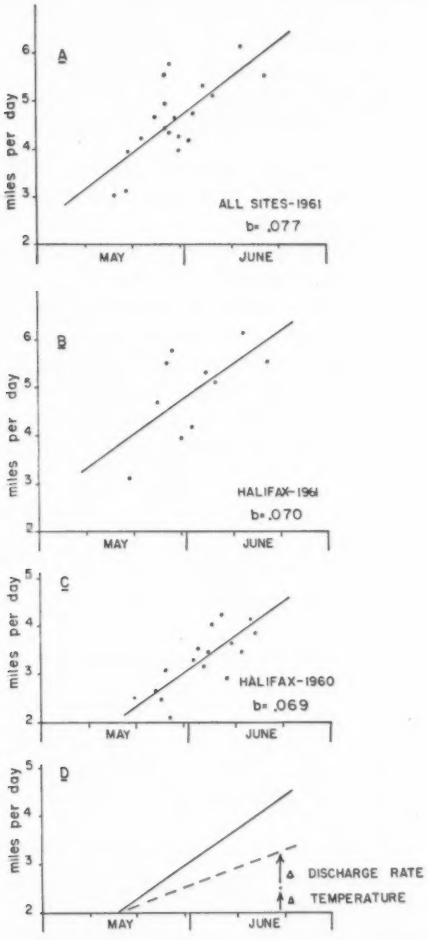

FIG. 4. Rates of travel on most direct route from tag and release sites to the outlet recovery site showing regression lines and regression coefficients. *A*. All tag releases, 1961. *B*. Halifax tag releases, 1961. *C*. Halifax tag releases, 1960. *D*. Solid line is the regression line of *C*; broken line shows the increase in rate of travel which might have been expected as a result of both increasing temperature and discharge rate during this period, 1960.

in rates of travel to the outlet from the three tag release sites of 1961, the adjusted means being:

Halifax to outlet	4.9 miles/day
Morrison to outlet	4.9 miles/day
Sandspit to outlet	4.6 miles/day
and, the overall 1961 mean	4.8 miles/day.

We might next inquire if these rates of travel as indicated by tagging are reasonable with respect to the swimming abilities of this species and the diurnal and seasonal timing of the migration.

The cruising speeds of sockeye salmon smolts as determined experimentally (Brett *et al.*, 1958) indicate that smolts of the size and in the temperature range with which we are dealing are capable of sustained swimming speeds of 0.8 to 1.1 ft/sec. Direct measurements of the actual speed of near-surface, migrating schools made at Babine Lake during 1960 and 1961 showed speeds ranging from .65 to 1.0 ft/sec with a mean of 0.8 ft/sec. To accomplish the rates of travel to the outlet shown by tagging, these fish would have had to swim on direct course at this speed (0.8 ft/sec) for a total of 6½ hours (1960) to 8½ hours (1961) each day.

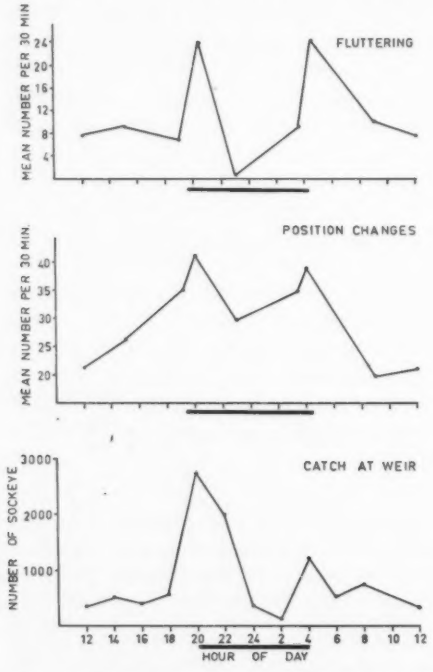

FIG. 5. Diurnal distributions of Fluttering and Position Changes (after Groot, unpublished data); total catch at lake outlet during migration (after Brett and Alderdice, 1958).

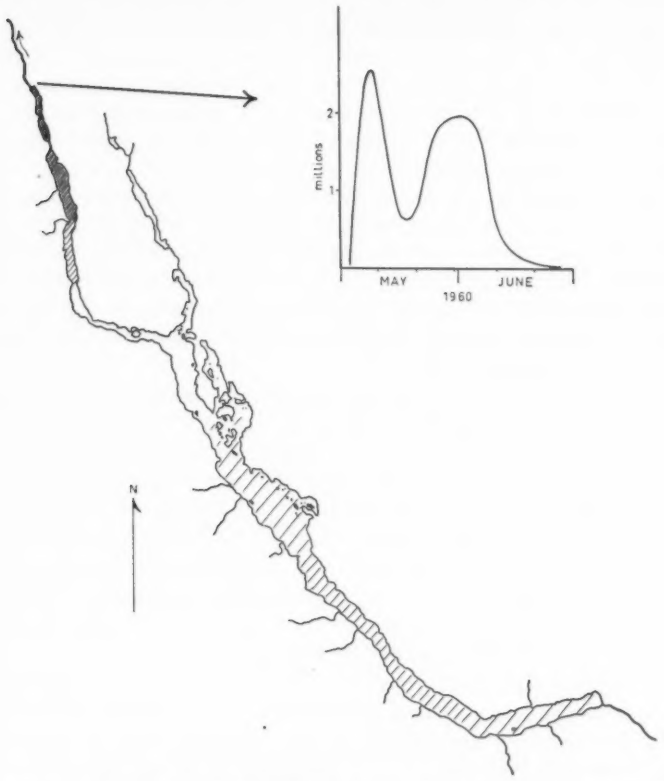

FIG. 6. Map showing the distribution of sockeye prior to migration and graph illustrating their migration from the lake as estimated at the outlet.

A number of sources give evidence that approximately this number of hours of each day is spent in active migration. Figure 5 shows the diurnal variations in two activities indicative of migration as observed in aquaria-held smolts. Both fluttering and position changes show diurnal peaks at dusk and dawn. The exodus of smolts from lakes as shown by catches at the outlet characteristically show peaks at dusk and dawn — the dusk peak being by far the greatest. Direct observation of near-surface migratory activity in the lake itself also verifies this. Migration may, of course, be proceeding at greater depths; however, the consistent evidence of hundreds of migrating schools suggests this near-surface migration around dusk and continuing into darkness as the major phenomenon. Certainly the lake migration is not going on continuously; most near-surface schools observed during the day are either stationary or moving slowly and randomly and are obviously feeding (as shown by stomach contents).

Figure 6 again shows the lake distribution of sockeye prior to the 1960 migration together with a graph of the seasonal variation in numbers of smolts

leaving the lake as estimated at the outlet. The first smolts left the lake on May 3 and their rate of exodus in the next few days increased explosively and then declined again after May 10. During this early peak of exodus, from May 4–12, an estimated 14 million smolts passed the outlet; they were fish of small mean size and obviously originated from the heavily populated basins nearest the outlet. The rate of out-migration remained relatively low from May 13–23 (during which an estimated 6 million passed the outlet) followed by a second peak, from May 23 to June 9, when an estimated 25 million passed downstream. This later peak obviously originated from the furthest uplake regions as evidenced by (1) decreasing lake catches reflecting an emptying of the North Arm as the early peak progressed, and (2) increased lake catches and the manifestation of increased near-surface migration activity directed toward the outlet in the North Arm–Halifax Narrows region after May 18.

If all smolts commenced their migration at the same time and travelled on a quite direct route to the outlet at the average speed of 3.2 miles per day shown by tagging, this picture of their rate of exodus at the outlet is approximately what would be expected. For, the near-outlet concentration of smolts would peak within a few days and the second peak from the furthest uplake concentration (centered about 75 miles uplake) would be expected about 23 days later.

The 1961 exodus from the lake (from a similar lake distribution) followed a similar pattern except that the second peak followed sooner after the first. This appears reasonable from the faster mean rate of travel of uplake smolts to the outlet in 1961 than in 1960 as shown by tagging.

All evidence indicates that the migration of smolts through the lake to the outlet is an active and well-oriented migration on a quite direct route to the outlet. Also, it appears that commencement of the migration from all lake regions is triggered at about the same time — likely by a common stimulus.

EVIDENCE OF THE MECHANISM OF ORIENTATION

What are the possible guiding cues used by these fish in keeping "on course" to the lake outlet? Whatever it is it must be, at least in large part, innately known, for they are migrating for the first time to a goal where they have never been.

The possibility of current as the guiding mechanism appears eliminated by a number of factors: (1) we have made numerous simultaneous observations on the direction of the near-surface migration activity and near-surface currents and no relationship is shown; active migration on the route leading to the outlet persists irrespective of current direction (Fig. 7), (2) there simply is no direct current throughout the lake oriented with respect to the outlet, (3) as pointed out by Hasler (1960) and Verwey (1958), current as a guiding mechanism can likely be eliminated *a priori* for pelagic, near-surface fish. Current, of course, may have a drift effect much as the wind does for birds; it has been shown likely that current may cause passive displacement and concentration of young sockeye during their lake life (Johnson, 1961).

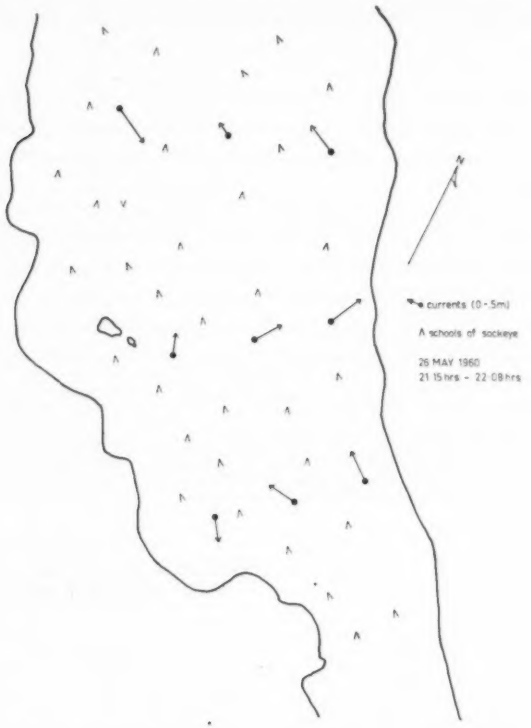

FIG. 7. Simultaneous observation of near-surface currents and direction of movement of near-surface migrating schools of sockeye in the lake basin immediately north of Halifax Narrows—2115 to 2208 hr, May 26, 1960.

The possibility of using shoreline, depth contours or horizon outline as primary guiding cues seems remote: the first two because we have found no relation whatever between them and the near-surface migration as observed; the third because of a lack of any landmarks which (at least viewed by a person from a boat on the lake) would give any indication of the direction of the outlet. However, there are some indications that shoreline and/or horizon outline may function as secondary guiding cues; and, of course, shoreline must at times become a barrier to further movement in a given direction.

In view of the importance of celestial orientation in animal migration shown in recent years, and especially the work of Hasler and his associates with sun-orientation of fishes, the celestial orientation ability of sockeye smolts has been examined. Groot (MS) has demonstrated that sockeye salmon smolts are able to use celestial phenomena to orient themselves in a certain preferred compass direction during a number of hours of the day; hence, a time-compensated celestial orientation mechanism is apparent. It is not yet clear which of the

celestial phenomena is used for this orientation. Better orientation with clear than with cloudy skies, and tests involving mirrors and artificial overcast conditions, indicate that the sun may be one of the most important celestial points of reference. On the other hand, good orientation during the dusk period, when migration appears most active, suggests that other celestial phenomena might be involved. However, the particular point or points of celestial reference are not of concern here.

As it is not possible to report here the full documentation collected on the orientation under experimental conditions of the Babine Lake sockeye smolts, we will confine ourselves to illustrating some demonstrative graphs. Full details will be given in a later paper by the second author.

During the 1960 migration of smolts through Babine Lake, directional preferences with a view of the sky only were tested at three different locations: Nilkitkwa Lake, Halifax Narrows and Morrison River (Fig. 8). When the data are separated into those obtained with relatively clear skies (0–60% cloud cover) and relatively overcast skies (70–100% cloud cover) it can be seen that under the former condition the fish from Nilkitkwa Lake and Morrison Arm showed directional preferences that correlate in general with the direct route to the

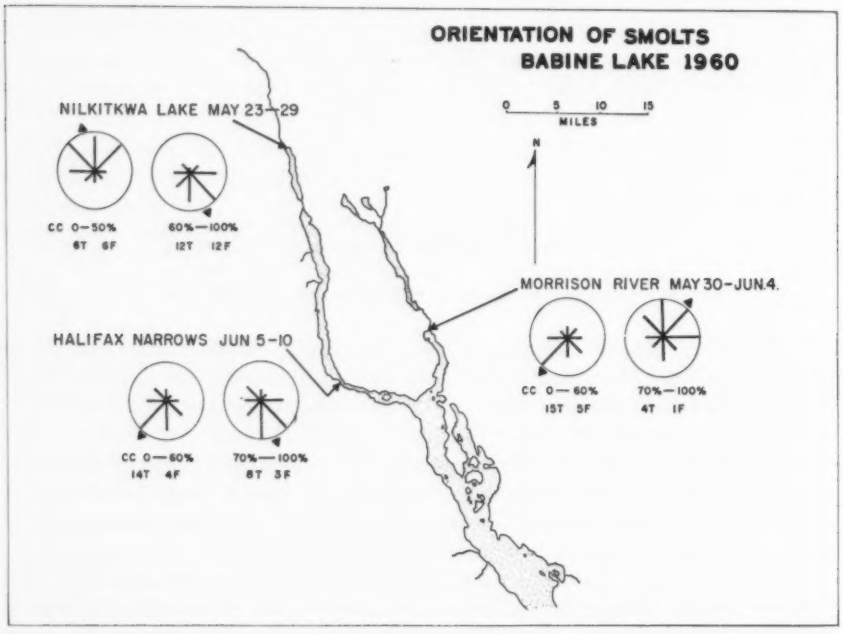

FIG. 8. Directional preferences of smolts with view of the sky only captured and tested at 3 different locations in 1960. The results are separated as to those obtained with relatively clear skies and those obtained with relatively overcast skies. Under each diagram the number of tests (T) and the number of smolts tested (F) are shown. (▶) The mean choice of directions. (CC) Cloud cover. For information on the construction of the diagrams, see methods.

outlet. In the case of the Halifax smolts it can be reported that when the data of each of the three observation periods are compared separately, a northwest directional preference is found during the dusk period, the time when the smolts are migrating most actively. (In most other cases orientation during the three observation periods did not vary significantly.) Further, it can be noted that in case of the smolts from Nilkitkwa Lake and Morrison River, orientation with overcast skies tends to be in the opposite direction of those with relatively clear skies. In general it has been found for sockeye smolts that the more the view of the sky is reduced or obstructed, naturally or artificially, the more such "reversed orientation" seems to occur. When the view of the sky is completely obstructed, random orientation or orientation to cues of the tank usually results.

During the 1961 smolt migration season, orientation of smolts was tested again at the three different locations mentioned above. Since it was found during

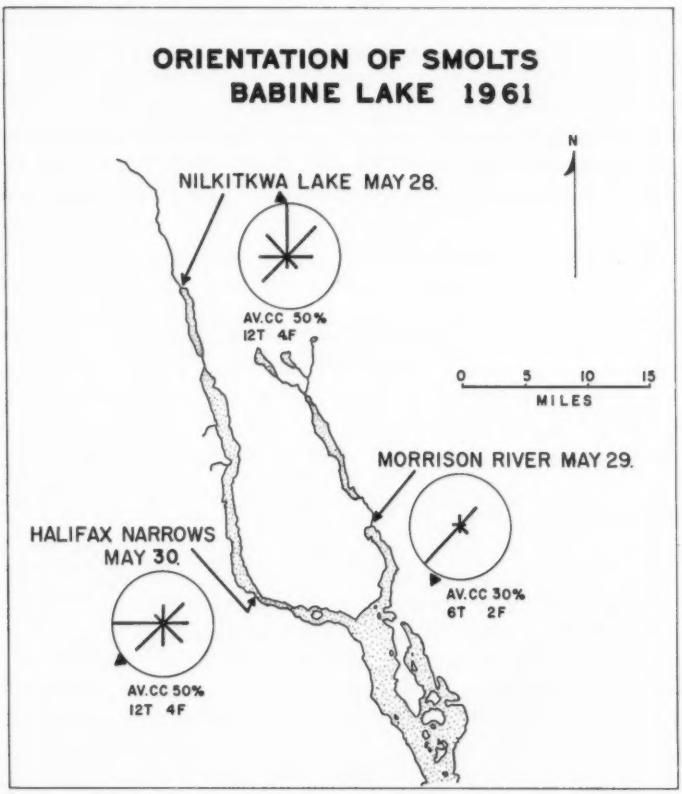

FIG. 9. Directional preferences of smolts, 1961, with view of the sky only at the same 3 places as in 1960 (see Fig. 8) and during about the same time of the season. (▶) The mean choice of directions. (T) Number of tests. (F) Number of smolts tested. (Av. CC) Average cloud cover.

the 1960 season, and in numerous other tests with smolts from other lakes, that best results can be expected with relatively clear skies, tests in 1961 were concentrated as much as possible during days with little cloud cover. Figure 9 shows the preferred direction of smolts in 1961 for dates corresponding nearest to dates of the 1960 tests. It is apparent that the conclusion drawn from the 1960 data still holds; namely, that the preferred directions shown under experimental conditions correlate in general with the shortest routes to the outlet.

For most of the sockeye smolts of this lake system, continued swimming in a northwesterly oriented direction would lead them on a rather direct route to the outlet. As shown above (Fig. 8 and 9), tests of smolts at Nilkitkwa Lake and Halifax Narrows show orientation in a west-northwesterly direction. The few tests carried out thus far at the far uplake Sandspit tagging site (Fig. 3) also indicate orientation in a northwesterly direction. Furthermore, orientation tests at Nilkitkwa Lake throughout the entire migration period show a constant one-directional preference for a northwesterly direction. In other words, it appears that simple one-direction (celestial?) orientation is involved, similar to that demonstrated for juvenile or unexperienced birds in their migrations (Perdeck, 1958; Verwey, 1958).

On the other hand, such one-direction orientation is not sufficient to explain the migration of the smolts from Morrison Lake to the outlet of Babine Lake on the rather direct route suggested by the tagging results, for these smolts must

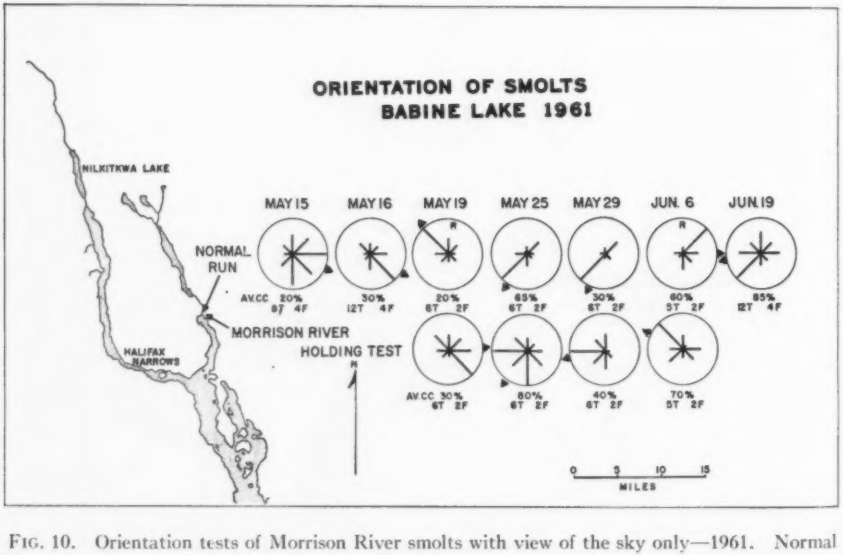

FIG. 10. Orientation tests of Morrison River smolts with view of the sky only—1961. Normal run: smolts taken and tested at the Morrison River site at intervals during the run. Holding test: smolts taken at Morrison River on May 16 and held there and tested periodically through June 6. (▶) The mean choice of directions. (T) Number of tests. (F) Number of smolts tested. (Av. CC) Average cloud cover. (R) Indicates probable reversed orientation.

make a complete 180° shift in direction from southeast to northwest in the course of their migration.

Groot (unpublished data) has evidence that sockeye smolts from another lake in British Columbia showed a change in the preferred direction with time, and so more detailed tests were conducted with Morrison River fish during the 1961 season. Smolts migrating from Morrison Lake through Morrison River to Morrison Arm were caught and tested periodically as the run progressed. Further, some fish were taken from the early part of the run and held throughout the migration period; these fish, held in a tank with a view of the horizon and the sky, were tested at the same times as those taken from the normal run. Figure 10 gives diagrams with direction preferences of the two groups of smolts. It can be seen that both the smolts taken from the normal run and those taken early in the run and held over, show a shift in direction preference with time: in the former, from about southeast to west; and in the latter, from about southeast to west-northwest. Perdeck (1960) has suggested a more or less similar phenomenon for chaffinches on the basis of observations of standard directions of flight on their migration route from Scandinavia to England via Holland, Belgium and France. For the Morrison smolts the biological significance of such a shift in directional preference with time is obvious: swimming first in a southeast direction would lead the fish out of Morrison Lake and down Morrison Arm, then a shift over south to southwest, west, and northwest would bring them into Halifax Narrows and through the North Arm to the outlet.

Figure 10 shows further that smolts tested earlier in the run than during the 1960 season showed directional preferences (southeast instead of southwest) that correlate better with the compass direction of Morrison Lake and the first part of Morrison Arm. When the smolts were tested in 1960 (Fig. 8) they apparently already had shifted their directional preference from southeast to southwest. This conclusion is also supported by the fact that when directional preferences of the Morrison smolts at a given time in 1960 are compared with smolts at the corresponding time in 1961, very similar preferred directions are found (Fig. 9).

In a few occasions "reversed orientation" occurred in the Morrison River tests (Fig. 10, normal run May 19 and June 6). Since a smaller tank was being used in 1961 (12 inches in diameter) as compared with 1960 (40 inches in diameter), these "reversed orientations" are thought to be possibly due to experimental conditions. Further tests in the following years will bear out if this conclusion is correct. It should be noted, however, that occasionally, during field observations in Morrison Arm and North Arm, schools were seen migrating in the opposite direction to the main bulk of schools, seldom in directions at right angles to the main direction.

More evidence of shifting in preferred direction of the Morrison River smolts has been obtained from fish tagged and released at Morrison River and later on recaptured at Halifax Narrows and Nilkitkwa Lake and tested at these sites (Fig. 11). When the directional preferences of the recaptured fish are compared with the directional preferences of fish from the same groups tested immediately

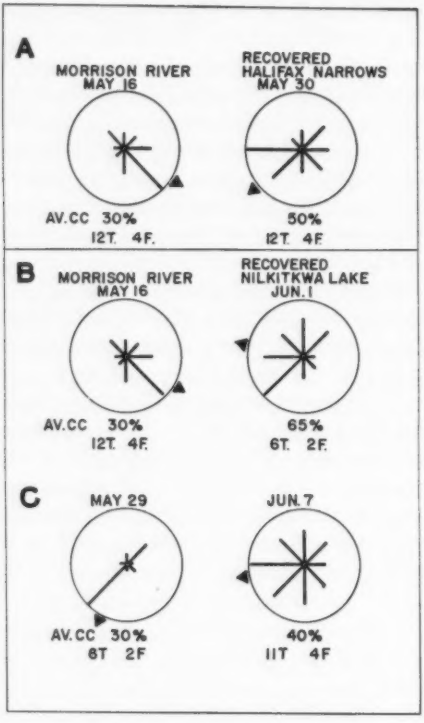

FIG. 11. A. Smolts tagged and released at Morrison River, then recaptured at Halifax Narrows and tested there. B. and C. Smolts tagged and released at Morrison River, then recaptured at Nilkitkwa Lake outlet and tested. (▶) The mean choice of directions. (T) Number of tests. (F) Number of smolts tested. (Av. CC) Average cloud cover.

after capturing them in Morrison River, it indicates that smolts that had migrated from Morrison River to Halifax Narrows had shifted their directional preference from about southeast to southwest and west, and those that had migrated all the way to the outlet had shifted between May 16 to June 1 from about southeast to north of west, and between May 29 to June 7 from about southwest to west.

Some further tests on the orientation of Morrison River smolts were carried out on a self-propelled barge while travelling over the migration route from Morrison River through Halifax Narrows into the North Arm in a few hours. In these tests, some fish were allowed a view of the sky only, and others a view of the sky plus horizon. No change in directional preference occurred with either group over the course of this journey. These results indicate the im-

probability of an innate knowledge of the topography of the lake and the improbability of bico-ordinate orientation (true navigation).

The evidence from orientation tests to date indicates that the complicated route followed by the Morrison River smolts in their migration to the outlet of Babine Lake can be explained by an inherent one-direction (celestial?) orientation which shifts with time of season from southeast clockwise to northwest.

The tagging data give some additional evidence of the general importance of celestial phenomena in orientation. It was noted above that the rate of travel of smolts to the outlet was significantly faster in 1961 than in 1960. Examination of the records of hours of sunshine at the nearest weather station (30 miles from the lake) (Fig. 12) shows that there were 376 hours of bright sunshine during the period May 1–June 20 in 1961 as compared to 296 hours for the same period in 1960. This might indicate that in 1961, with the sunshine record

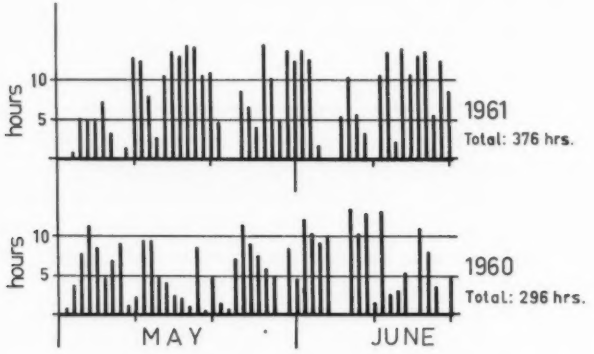

FIG. 12. Hours of bright sunshine per day at Smithers, B.C. (Canada Department of Transport, Meteorological Branch.)

indicative of more clear skies, the sockeye smolts were able to orient better and so keep on a more direct course to the outlet, thus showing a higher rate of travel. This is, of course, only a two-point correlation. However, further examination of this hypothesis is available by comparing the rates of travel shown from the various tag releases and the hours of sunshine on the days immediately following release. This relationship was examined for all releases in which the number of recaptures was 10 or more (Fig. 13). In each set of data, rates of travel were adjusted to the mean date based on the regression analysis. The number of days immediately following release date, which forms the basis for mean hours of sunlight, were as follows:

Halifax site:	5 days
Morrison site:	8 days
Sandspit site:	12 days

These periods were determined by distance to outlet and the time taken to cover the distance by the faster migrating fish as shown by tagging. As shown in Fig.

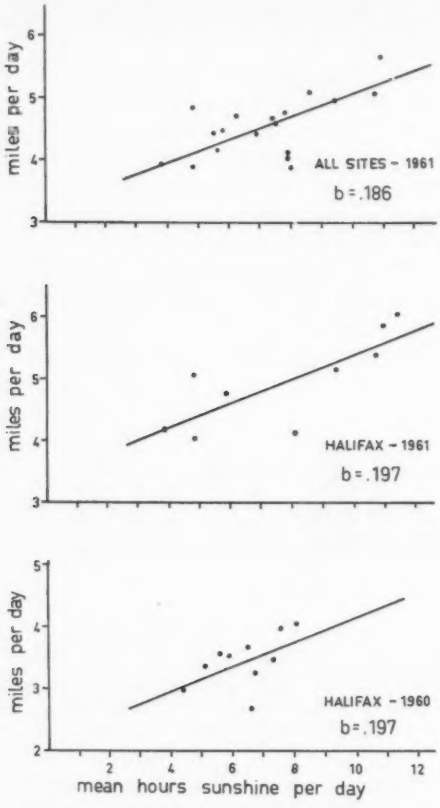

FIG. 13. Relationship between adjusted rates of travel on most direct route to outlet as shown by tagged fish and the mean hours of sunshine per day on the days immediately following release. Regression lines and coefficients are shown.

13, there is a positive relationship between mean hours of sunshine for the days immediately following release and rate of travel to the outlet. This evidence supports the view that celestial phenomena might be important as guiding cues in orientation during this migration.

CONCLUSIONS

Results to date lead us to the following conclusions:

(1) The migration of sockeye smolts from the nursery area to the outlet of Babine Lake is a well-oriented, non-random movement in the direction of the lake outlet, and its commencement from all lake regions occurs at about the same time, suggesting triggering by a common stimulus.

(2) The migration takes place principally at near-surface depths. Diurnally, most of the active migration is centered around the evening dusk period. Sockeye smolt schools move at a speed of 0.65 to 1.0 feet per second when migrating. The mean rate of travel of tagged fish per day was 3.2 miles in 1960 and between 4.6 and 4.9 miles in 1961.

(3) There is an increase in rate of travel from all parts of the lake as the season progresses; this increase cannot be accounted for by increasing temperatures and flow rates of the water alone. It is probably a reflection of increasing migration drive.

(4) There is a positive relationship between mean hours of sunshine for the days immediately following release of tagged fish and the rate of travel to the outlet.

(5) The possibility of current as a guiding mechanism can be eliminated; and the possibility of shoreline, depth contours or horizon outline serving as reference points for well-oriented movement in the direction of the lake outlet seems remote.

(6) Sockeye smolts have been found able to orient with a view of only the sky with the horizon blocked off. Thus a time-compensated orientation in relation to celestial phenomena is apparent. This implies the existence of an internal clock or diurnal rhythmic sense that allows the fish to make the proper adjustments to the diurnally and seasonally changing phenomena.

(7) The preferred direction shown under experimental conditions with a view of only the sky correlates in general with the compass direction of the shortest route through the lake to the outlet. This suggests the existence of apparently distinct stocks with inherited direction finding tendencies which correlate with the appropriate routes to the outlet.

(8) In most cases, continued swimming in one preferred direction (northwesterly) would lead the fish to the outlet. The Morrison River smolts, however, show a directional preference which shifts with time of season from southeast to northwest. The complicated route of the Morrison Lake smolts can be sufficiently explained by this shifting one-direction (celestial?) orientation and does not imply bico-ordinate navigation.

ACKNOWLEDGMENTS

We are much indebted to Drs J. R. Brett and M. P. Shepard of the Biological Station, Nanaimo, British Columbia, for their interest, help and positive criticism of the work at all stages. Furthermore, we are grateful to those who assisted us in the technical and experimental work, and in particular, Messrs F. Jordan, W. Wiley, D. Workman, T. Terhune, J. Kolodychuk, K. Vermeer, J. Smith, M. Healy, and K. Roy.

The second author wishes to express his great appreciation to Dr J. J. A. van Iersel of the University of Leyden, Holland, for his advice and helpful criticism, and for the highly stimulating, enjoyable, and profitable discussions on orientation problems during the past few years.

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A Model of Seawater Structure Near the West Coast of Vancouver Island, British Columbia[1,2]

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ABSTRACT

Oceanographic data collected in a line of stations extending seaward of the west coast of Vancouver Island, British Columbia, were reviewed and analyzed. On the basis of these data and the large-scale meteorological processes of wind, insolation, and precipitation, the characteristic structure of temperature and salinity in the coastal region was defined in five temporal stages throughout the year. These stages are presented as vertical sections along the line with characteristic ranges of values to be found in each of the structural elements.

INTRODUCTION

Temperature and salinity structures[4] in the coastal region off the southwestern coast of Vancouver Island, British Columbia (Fig. 1) have been reviewed by Lane (1962). A more detailed study of the data (Anon, 1957–1961) in this region has permitted the definition of five stages in the cycle of seasonal changes of the temperature and salinity structures.

The form of the model is a vertical section normal to the coast, from the shore to seaward of the continental slope. For convenience of description, the structures in the section have been simplified into their principal zones, idealized, and their features defined. Each zone defines a layer or depth interval in which the properties of the water are constant, or consistently change with depth, and whose limits are defined by features of structure rather than numerical values (Tully, 1949, p. 6; 1958, p. 528).

The five stages of salinity and temperature structure constitute a model which is believed to be applicable to the coastal region defined above, and also, to some degree, to the entire west-coast Canadian and Alaskan coastal regions.

The salinity structures in the local estuarine regions and the Subarctic Pacific Ocean have been described by Tully (1958), and by Tully and Barber (1960). An upper and a lower zone, in which the salinity structures are nearly isohaline, and which are separated by a halocline, were defined in both regions. By analogy, a simple temperature structure is defined here as upper and lower thermal zones separated by a thermocline.

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[2]Based on a thesis submitted in conformity with the requirements for the degree of Master of Science at Oregon State University.

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[4]Following the usage of Tully (1958, p. 528) the term structure refers to the distribution of properties of the water, usually in the vertical sense. A graph of salinity as a function of depth (cf. e.g. Fig. 2) or a plot of the isopleths of salinity in a section defined by length and depth defines the salinity structure.

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SEASONAL FACTORS CONTRIBUTING TO STRUCTURE

The five stages of the model are related to the seasonal variations of runoff, heating and cooling, and wind, the factors determining the character of the coastal waters. The annual cycles of precipitation, runoff, insolation, and wind velocity and strength in this region have been discussed (Lane, 1962, pp. 51–64). These are briefly reviewed here and the factors pertinent to the discussion of each stage of the model are appropriately included therein.

RUNOFF

Fresh water enters this region (Fig. 1) mainly as discharge from small local rivers, e.g. the Stamp River (as shown in Fig. 2), and larger continental rivers, e.g. the Fraser River (as shown in Fig. 2). The former, subject to a summer discharge from the melt of highland snow storage, as well as the stronger, precipitation-induced (Fig. 3a) winter discharge, shows two maxima. The 1957 data show the second peak especially well. The Fraser River data reflect the single summer maximum discharge from the melt of continental snow-fields. Both sources of fresh water enter the sea as estuarine discharge, resulting in a brackish upper zone.

Tully (1958) has shown that there is unidirectional upward transfer of salt (entrainment) from the more dense oceanic water to the overriding estuarine discharge when there is a velocity shear between the zones. Further, he showed that the greatest shear occurred in the halocline. It has also been shown (Tully and Barber, 1960) that the features of the estuarine structures are similar to

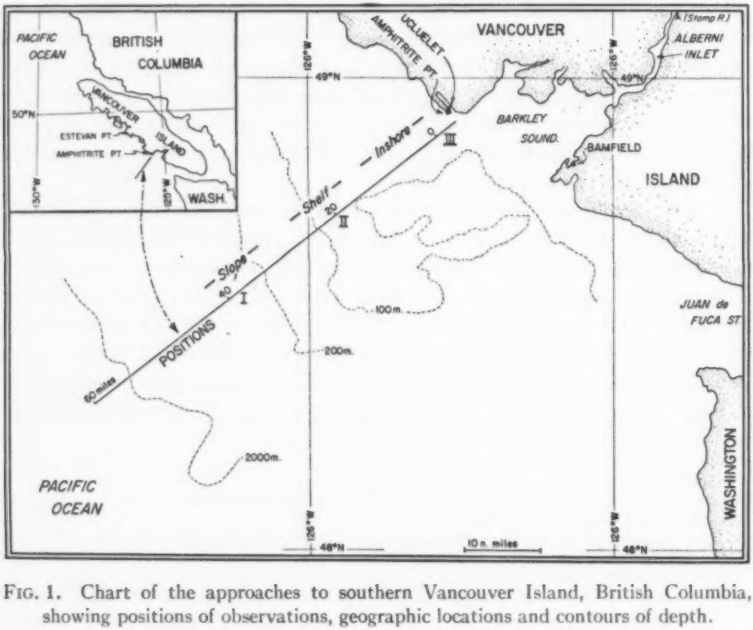

FIG. 1. Chart of the approaches to southern Vancouver Island, British Columbia, showing positions of observations, geographic locations and contours of depth.

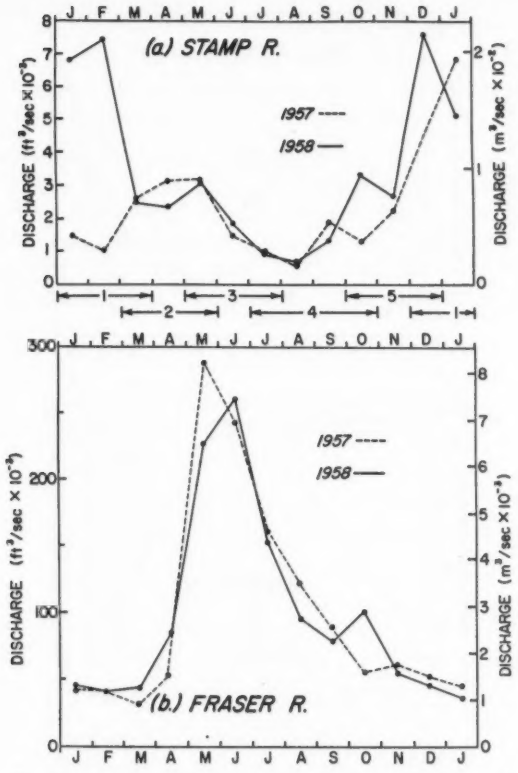

FIG. 2. Mean monthly discharge of coastal (Stamp) and mainland (Fraser) rivers, 1957–1958.

those found in the Subarctic Pacific Ocean. Velocity shears caused by oceanic mechanisms, such as convergence and divergence, may result in a demand for lower-zone water and, hence, entrainment.

HEATING AND COOLING

Tully and Giovando (1963) have discussed the growth and decay of the seasonal thermocline in the neighbouring Subarctic Ocean in considerable detail. They show that during the heating season from late March to mid September the net daily heat gains are mixed downward to the limit of wind-generated turbulence. This results, as shown in idealized form in Fig. 4, in a warmed wind-mixed upper zone separated by a thermocline from the underlying unwarmed waters. The bottom of the thermocline defines the limit of the surface heating and wind mixing processes.

During the cooling season (mid September to late March) there is a net heat loss, evaporation increases and convection becomes appreciable. In consequence the upper-zone waters cool and the thermocline is eroded and sinks and finally vanishes at the end of winter.

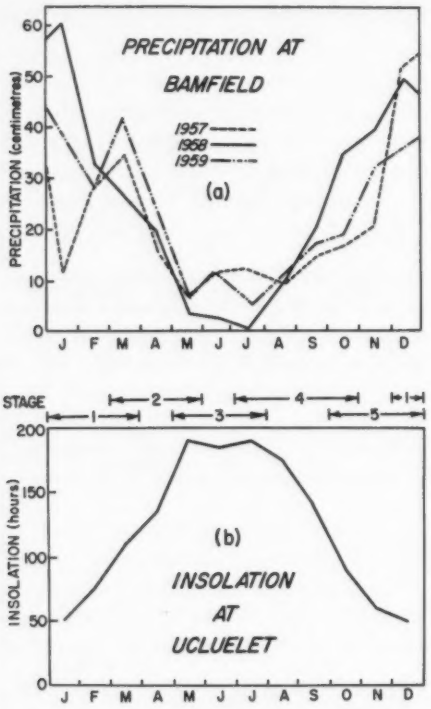

FIG. 3. (a) Monthly totals of precipitation (1957–1959) on the west coast of Vancouver Island (Bamfield, B.C.) (Fig. 1). (b) Mean monthly hours of bright sunshine on the west coast of Vancouver Island (Ucluelet, B.C.) (Fig. 1). (After Climatological Atlas of Canada, 1953, National Research Council of Canada.)

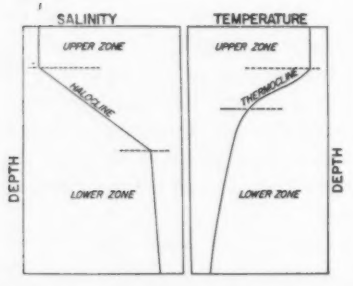

FIG. 4. Definitions of temperature and salinity structure.

Wind

The transfer of momentum from the winds to the sea causes local turbulence (mixing, which has been noted) and transports the near-surface waters to the right of the wind in these latitudes (Sverdrup *et al.*, 1942).

In this locality the winds blow predominantly from the northwest during summer (Lane, 1962) (Fig. 5), driving the surface waters seaward, with consequent divergence along the coast. When local estuarine discharge is not adequate to replenish this divergence, upwelling (Sverdrup, 1938) occurs (deep water rises to the surface) (Fig. 6). Pickard and McLeod (1953) attribute the occurrence of unseasonably cold water along this coast during the summer to this divergence process.

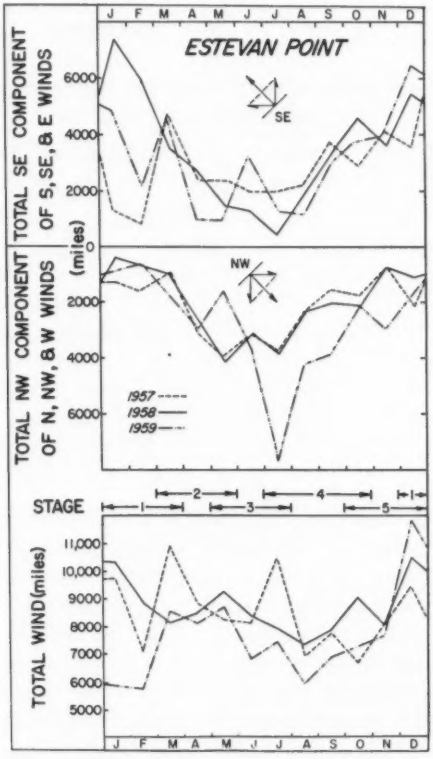

Fig. 5. Winds along the west coast of Vancouver Island (Estevan Point, B.C., Fig. 1). (*Upper*) Components of wind mileage resolved from the southeast and northwest (1957–1959), by months. (*Lower*) Total wind mileage (1957–1959), by months.

During the winter, the winds blow predominantly from the southeast, creating a convergence situation (Fig. 6) in which surface waters are conserved along the shore.

The oceanographic structures in these coastal waters, associated with these seasonal wind-induced situations are distinct.

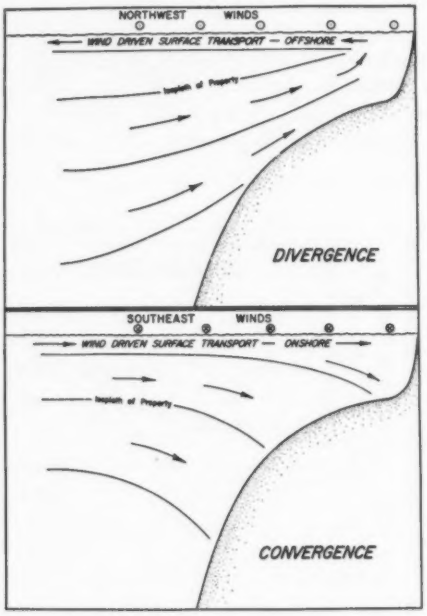

FIG. 6. Conditions of divergence and convergence in British Columbia coastal waters.

THE MODEL

By combining the seasonal sequences of estuarine discharge, heating and cooling, and wind direction, a multiplicity of situations may be defined. However, from consideration of the data it has been possible to reduce these to five principal stages analogous to seasons. Each stage may be defined, in a climatic sense, by the predominant states of the factors. Like the seasons, the time limits of the stages are not exact; rather one stage gradually changes to the next, and from year to year may be earlier or later than the average. Hence, in the following descriptions there are some overlaps in the dates, signifying periods of transition or indeterminacy.

STAGE 1 (DECEMBER THROUGH MARCH)

During this period, the winds are predominantly from the southeast and the monthly wind mileages are maxima (Fig. 5). Precipitation (Fig. 3a) and the corresponding runoff through local estuaries (Fig. 2) are also at their annual maxima.

SALINITY. An example of observed salinity structure is shown in Fig. 7a. In the shallow water, the salinity structure is strongly developed only near the shore. In the oceanic part of the region the waters are isohaline to at least 50 m depth. The isohalines slope downward toward the shore, particularly in the inshore region.

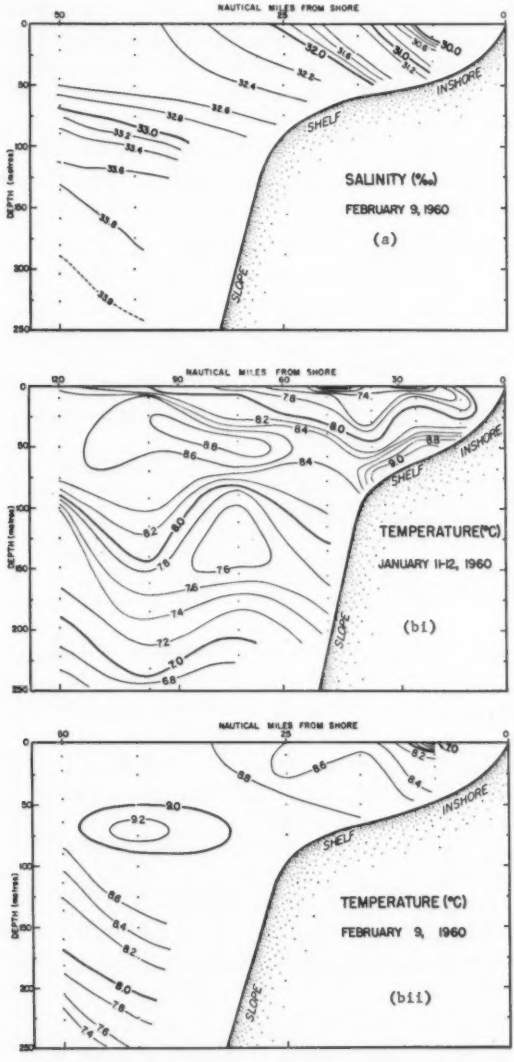

FIG. 7. Examples of salinity and temperature structure in a section seaward of Amphitrite Point, B.C. (Fig. 1) during Stage 1.

The force of the wind results in deep mixing throughout the entire oceanic and coastal region except near shore, where the large coastal discharge provides continuous renewal of brackish water and large stability. An onshore movement produced by the strong southeast winds confines the brackish discharge from local estuaries (e.g. Barkley Sound) to a narrow, northward flowing, alongshore stream (Barber, 1957, p. 947; Lane, 1962, p. 86). The relative intensities of wind and discharge determine the width of the brackish coastal water belt.

An idealized model of the type of salinity distribution and plots of structures in the section are shown in Fig. 8a and structures observed in each part of the section are shown in Fig. 9.

The isohaline oceanic upper zone (OU) in the slope region is 50–70 m deep with a characteristic salinity range of 32.2–32.6 ‰. The oceanic halocline extends below this in two distinct sections (OH_1 and OH_2) (Fig. 8a, 9a(i)) to about 200

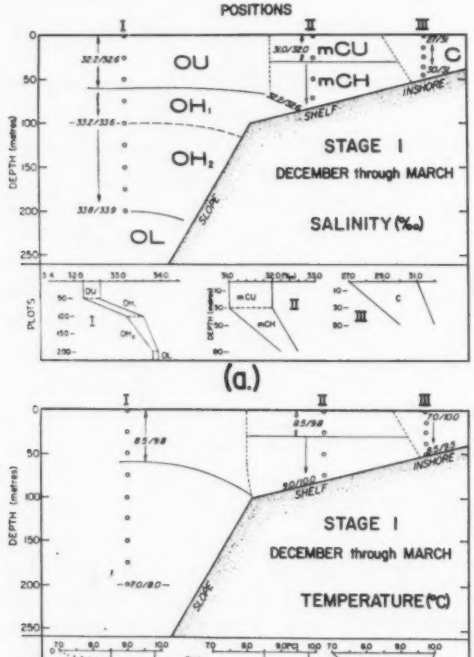

FIG. 8. Model of structure and distribution in a vertical plane seaward of Amphitrite Point, B.C. (Fig. 1) and *plots* of structures showing ranges of values at positions I, II and III (Fig. 1). (a) Salinity, Stage 1. (b) Temperature, Stage 1.

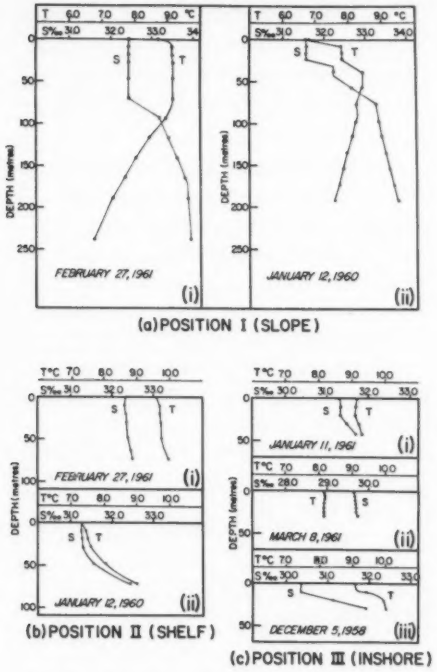

FIG. 9. Examples of data in: (a) position I, (b) position II, and (c) position III during Stage 1 (Fig. 8).

m depth. At this limit the salinity becomes 33.8–33.9 ‰. In this paper, the oceanic halocline will be considered as a single feature (OH). The oceanic lower zone (OL) lies below the halocline, and in it the salinity increases slightly toward the sea bottom.

Normally, the shelf (Fig. 7a) is a transition region containing a modified coastal upper zone (mCU) (Fig. 8a) and a modified coastal halocline (mCH) extending to the bottom (Fig. 9b(ii)). This is indicated in plot II (Fig. 8a). The salinity is 31–32‰ in the upper zone, and increases in the halocline to 32.2–32.6 ‰.

At times there has been evidence of low-salinity coastal waters in the oceanic upper zone over the edge of the continental shelf (Fig. 9a (ii)). Such a condition seems likely to be associated with the infrequent periods of off-shore flow created by northwesterly winds. Also there are times when the oceanic upper zone may intrude over the continental shelf because of the convergence mechanism associated with strong southeasterly winds. When this occurs the water over the continental shelf becomes homogeneous (Fig. 9b(i)).

Plot III (Fig. 8a and Fig. 9c) shows the large range of values and structures to be found in the inshore coastal (C) waters. Continual replenishment of the

brackish water from estuarine discharge (Fig. 3) usually maintains the structure in which the salinity increases with depth, despite wind and tidal mixing. A mixed upper zone, sporadically created by the wind, may be present. Surface salinities range from 27–31 ‰ while near the bottom the values range from 30–31 ‰.

TEMPERATURE. During this period winds are strong (Fig. 5), insolation is minimum (Fig. 3b), and surface cooling is maximum. The consequences are indicated in the examples of observed data shown in Fig. 7b(i) and (ii). In both diagrams, surface temperatures are low. However, inshore stability has inhibited mixing over the shelf so that temperatures decrease shoreward.

In both diagrams, the isotherms slope downward to the coast. Figure 7b(i) indicates this most clearly. First, the isotherms slope more steeply and more definitely downward toward the coast. Second, the more stable coastal water is confined more closely to the shore and the well-mixed oceanic upper zone dominates the slope region and seaward.

The idealized model of temperature distribution in the seaward section, and "plots" of the structures are shown in Fig. 8b, and structures observed in each part of the section are shown in Fig. 9.

In the slope and offshore part there is an isothermal upper zone, more than 50 m deep, coincident with the salinity upper zone (Fig. 9a (i)). The temperatures range from 8.5 to 9.8° C. Doe (1955, p. 12) found that surface temperatures decreased to seaward from this region in winter. At the bottom of the upper zone there is frequently a temperature maximum (Fig. 7b (i)) which is considered a transient feature, although it is recurrent. Below this zone (Plot I, Fig. 8b) the temperatures decrease uniformly with depth to values between 7 and 8° C at 200 m depth.

In the shelf and inshore parts of the section the structures are isothermal or increase with depth. It appears that the positive temperature structure is the more common.

The temperature of the bottom waters is at its annual maximum during this season. It is reasoned that this water is the remnant of upper zone oceanic water which was warmed during the previous seasons. During the winter it is conveyed shoreward and depressed by the convergence mechanism, and partly cooled. It is overlaid by estuarine-discharge waters which are stable because of their low salinity, and colder because they are subject to surface cooling. Plot II (Fig. 8b) shows the general structure, which is exemplified in Fig. 9b (ii). The upper zone (0–30 m depth) may be as cold as 7° C when estuarine water is present. More frequently the values range from 8.5 to 9.8° C. Bottom temperatures range from 9 to 10° C.

In the inshore waters (Plot III, Fig. 8b) a wide range of temperature structures may be found. The waters may be isothermal, or positive or negative thermoclines may exist, depending on the properties of the brackish estuarine discharge that is present (see examples in Fig. 9c). In this part of the region the range of temperature at the surface is 7–10° C and at the bottom is 8.5–9.5° C.

STAGE 2 (MARCH THROUGH APRIL)

During this period the coastal runoff (Fig. 2) is less than during Stage 1 and insolation (Fig. 3b) increases. Wind velocities (Fig. 5) are still large but the direction is variable because this is a period of change from dominant southeast to dominant northwest winds. This results in a relaxation of the convergence mechanism and allows surface waters to extend seaward.

SALINITY. An example of the observed salinity structure is shown in Fig. 10a. The winter accumulation of brackish coastal water spreads seaward over the oceanic water previously present. This event may occur in varying degrees depending on the nature of the wind and the amount of coastal water. Alternating periods of northwest and southeast winds and periodic, tidal-controlled, discharges from the estuaries may result in the formation of isolated pools of brackish water in this region (Lane, 1962, pp. 67 and 71).

During this period the isohalines still bend downward toward the coast, particularly in the shelf part of the section. In the oceanic part the slope is much less than during the winter.

The model of salinity distribution and structures (plots) is shown in Fig. 11a, and structures observed in the several parts of the section are shown in Fig. 12.

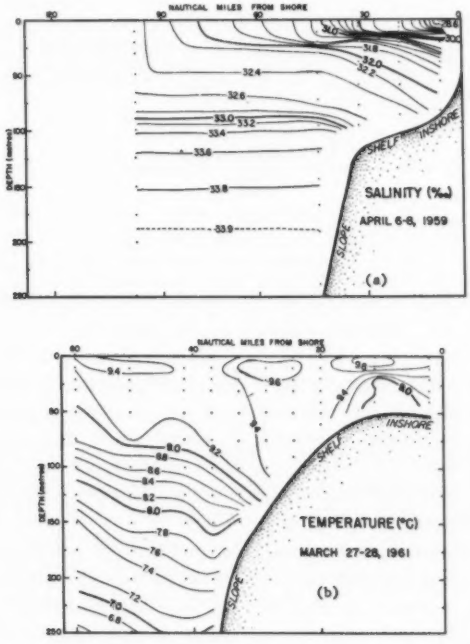

FIG. 10. Examples of temperature and salinity structure, Stage 2.

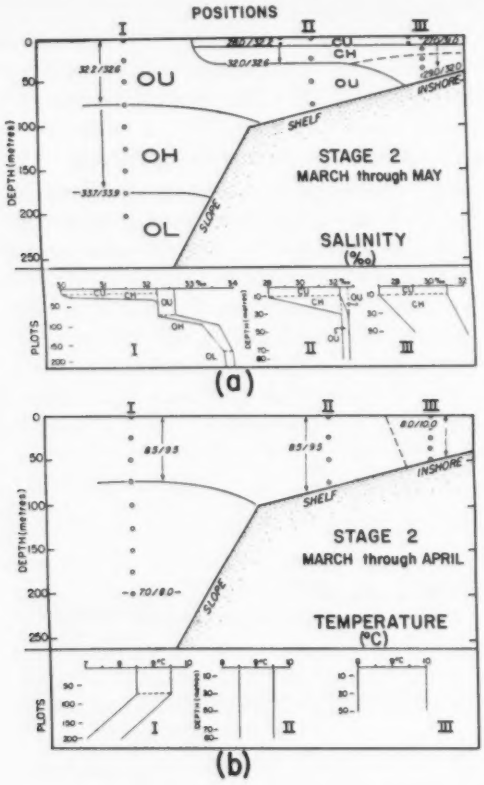

FIG. 11. Model of structure and distribution in a vertical plane seaward of Amphitrite Point, B.C. (Fig. 1) and *plots* of structures showing ranges of values at positions I, II and III (Fig. 1). (a) Salinity, Stage 2. (b) Temperature, Stage 2.

In the oceanic and slope parts of the section the three salinity zones are apparent and are defined by the structure and range of values as in Stage 1. The oceanic upper zone (OU) extends to about 75 m depth and is continuous over the shelf. Below this the oceanic halocline extends to about 175 m depth. This rise from the depth (200 m) found in Stage 1 is attributed to the relaxation of the winter convergence mechanism.

In this Stage 2, the coastal waters (CU and CH) may extend further seaward and override the oceanic upper zone in the shelf and slope parts of the section. This coastal water contains a shallow (10 m) homogeneous upper zone (CU) and a halocline (CH) which extends to about 30 m depth. Thus, as shown by the structures in Plots I and II, there may exist one halocline (OH) or two haloclines (OH and CH) in the slope part (Fig. 12a (ii) and a (i)), and one halocline

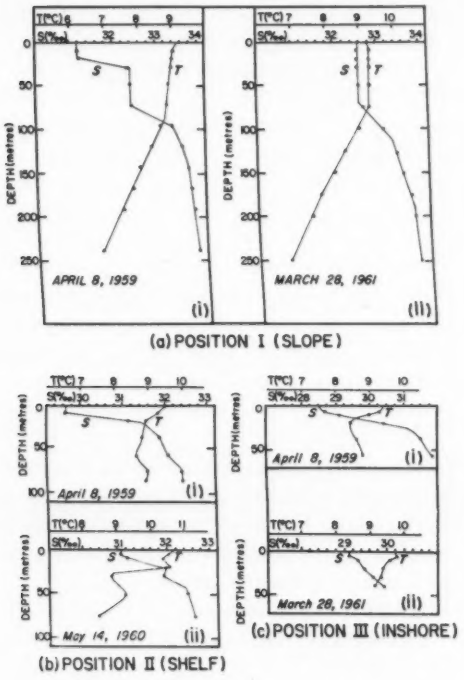

FIG. 12. Examples of data during Stage 2 (Fig. 11).

(CH) over the shelf (Fig. 12b). The coastal features are superimposed on the oceanic upper zone (OU) water and separate it from surface wind influence. Because of this and tidal mixing with the less saline coastal waters this lower (OU) water begins to lose its homogeneity (Fig. 12b (i) and (ii)).

Plot III (Fig. 11a) shows the low salinities in the inshore surface waters (27–31 ‰). Below this, coastal halocline (CH) water extends to the bottom. The inflow of brackish estuarine (runoff) water maintains the intense shallow halocline (Fig. 12c).

TEMPERATURE. During these months the insolation (Fig. 3b) increases gradually. The heating and cooling processes are nearly in balance (Tabata, 1961, p. 1107) and there is no appreciable change occurring in the thermal structure.

An example of observed temperature structure is shown in Fig. 10b. In general the upper waters are isothermal.

The model of temperature distribution and structure (plots) is shown in Fig. 11b and the structures observed in the several parts of the section are shown in Fig. 12.

In the slope part (Plot I, Fig. 11b) the isothermal upper zone reaches its maximum depth (about 75 m) coincident with the oceanic upper salinity zone (OU, Fig. 11a). Upper zone temperatures range from 8.5 to 9.5° C. Below this the temperature decreases uniformly to 7–8° C at about 200 m depth.

It will be noted that the Stage 2 temperature model (Fig. 11b) is shorter by one month than the Stage 2 salinity model (Fig. 11a). It is felt that while the shelf salinity structure undergoes marked changes during this period, the temperature structure remains quite similar to that shown in Stage 1 through April. Apparently, relative temperature homogeneity is achieved in the seaward flow of low salinity water in this stage (e.g. Fig. 12a (i)).

Inshore, the temperature structure is more closely associated with the salinity structure (Fig. 12c). Doubtless the stability inherent in the salinity structure prevents the downward dissipation of heat. Hence, any temperature increase, slight though it may be, is conserved in the upper 10–20 m of depth.

Stage 3 (May through July)

During this period the large mainland rivers are in freshet (Fig. 2b) due to the melting snow in the mountains. This reaches the region as an increased outflow of brackish water from Juan de Fuca Strait (Fig. 1). A lesser contribution of runoff comes from the secondary maximum of local estuarine outflow (Fig. 2a), which is also due to snow storage.

During this period the predominant winds are moderate from the northwest (Fig. 5). Hence the convergence mechanism is fully relaxed, and some instances of divergence may be expected.

Salinity. An example of observed salinity structure is shown in Fig. 13a. Here there is a marked shallow halocline lying horizontally. Obviously the water above this halocline is coastal water which extends seaward beyond the continental slope. Immediately below this shallow halocline to 75 m depth, the isohalines are inclined downward toward the coast, particularly over the shelf. Below 75 m depth, in the offshore part, the isohalines are inclined upward toward the continental slope.

The presence of a well defined brackish upper zone is sufficient evidence that the estuarine mechanism (Tully, 1949, p. 267; Tully, 1958, p. 524) is now an important feature in the behaviour of these coastal waters.

The model of salinity distribution and structure (plots) is shown in Fig. 14a, and the structures observed in the several parts of the section are shown in Fig. 15.

Coastal water (CU and CH) frequently extends seaward of the continental slope and occupies most of the depth of the oceanic upper zone (OU) (Plot I— dashed lines — Fig. 14a and 15a(i)).

There is a shallow upper zone (CU) 10–20 m deep extending from the inshore part of the section seaward of the shelf. At any position it is vertically isohaline (Fig. 15) due to normal wind mixing, but its salinity increases to seaward, as shown in the Figures, due to entrainment (Tully, 1949, p. 526). The coastal halocline (CH) is continuous through the three parts of the section. In the

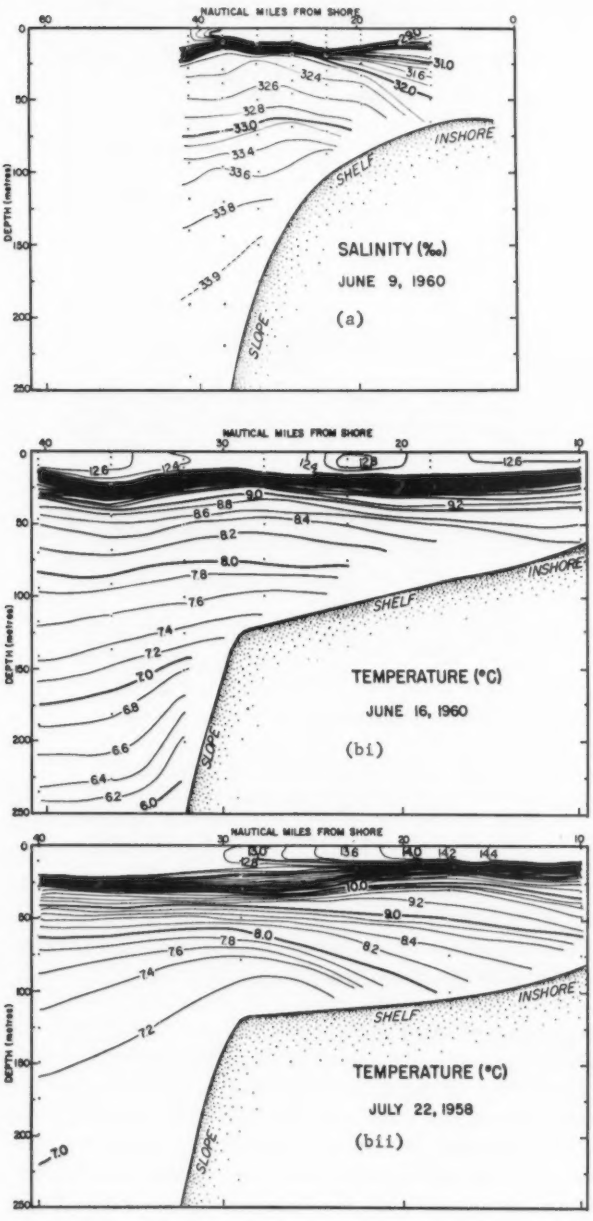

FIG. 13. Examples of salinity and temperature structure, Stage 3.

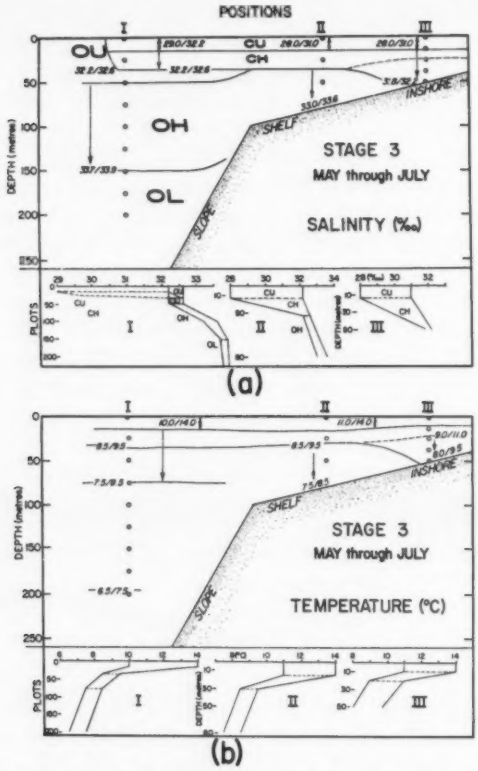

FIG. 14. Model of structure and distribution in a vertical plane seaward of Amphitrite Point, B.C. (Fig. 1) and *plots* of structures showing ranges of values at positions I, II and III (Fig. 1). (a) Salinity, Stage 3. (b) Temperature, Stage 3.

slope and shelf parts it extends to 30–40 m depth, and is limited by salinity 32.2–32.6 ‰. In the slope part of the section this is underlaid by the remnants of the oceanic upper zone (OU) which separates the coastal and oceanic haloclines (Fig. 15a (i)).

If the coastal water does not extend into the oceanic part of the section (Plot I — solid lines — Fig. 14a and 15a(ii)) then oceanic upper (OU) water occupies the upper 50 m of depth. In any case, below the layer of oceanic upper zone (OU) water, the oceanic halocline (OH) extends down to about 150 m depth. Its lower limit is marked by salinity 33.7–33.9‰. The rise of this oceanic halocline (OH) towards and onto the shelf is attributed primarily to the entrainment mechanism associated with the brackish upper zone. The condition of moderate winds, predominantly from the northwest, allows the convergence mechanism to relax, but may not be sufficient to create a divergence system.

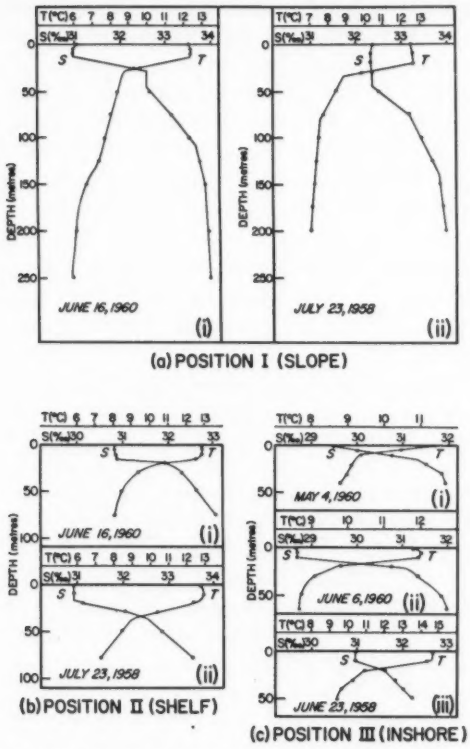

FIG. 15. Examples of data during Stage 3 (Fig. 14).

During this season it is most probable that coastal (C) rather than oceanic (O) water occurs in the upper 40 m over the shelf part of the section (Fig. 14a, Plot II). Below this, oceanic halocline (OH) water extends to the bottom. The lack of residual oceanic upper zone (OU) water between the two haloclines (Plot II, Fig. 14a, and Fig. 15b) indicates that it must have lost its homogeneous structure through mixing with the neighbouring zones. By reason of the overlying coastal water, the OU water is no longer influenced by the thorough-mixing effect of the wind. Hence, a velocity shear between it and the oceanic halocline (OH) below, is sufficient to cause mixing and the entrainment upward of OH water (the necessity for such velocity shear is discussed by Tully (1952, p. 271)). Hence, the rise of the oceanic halocline onto the shelf during this stage is probably not due to the divergence process, a mechanism not likely to be effective until the northwest winds become more prevalent. There is no reason, of course, why the OU water in the shelf region has not been mixed upward into the coastal/halocline water. Both mechanisms must be expected to have occurred, their relative effectiveness being dependent upon the relative velocity shears involved.

Inshore (Plot III, Fig. 14a) the coastal upper zone (CU) and halocline (CH) occupy the whole depth. Evidently the volume of estuarine discharge is sufficient to dominate this part of the section at this time of year. The halocline here may be generated by lateral entrainment (Tully, 1958, p. 526) or from points of local upwelling in the vicinity (Tully, 1942, p. 403). In any case, oceanic halocline (OH) water is seldom found inshore during this period.

TEMPERATURE. During May through July, insolation (Fig. 3b) and heating are maximum in this region. An isothermal upper temperature zone is formed to the depth of local wind mixing. This depth is limited by the pycnocline inherent in the halocline. In this upper zone the temperature increases progressively. Hence, the thermocline associated with the halocline grows in magnitude during the period. Below this, the temperature of the water is not affected by local surface heating.

Examples of observed temperature structure are shown in Fig. 13b (i) and (ii). Here the temperature structure is distinct and coincident with the salinity structure (Fig. 13a).

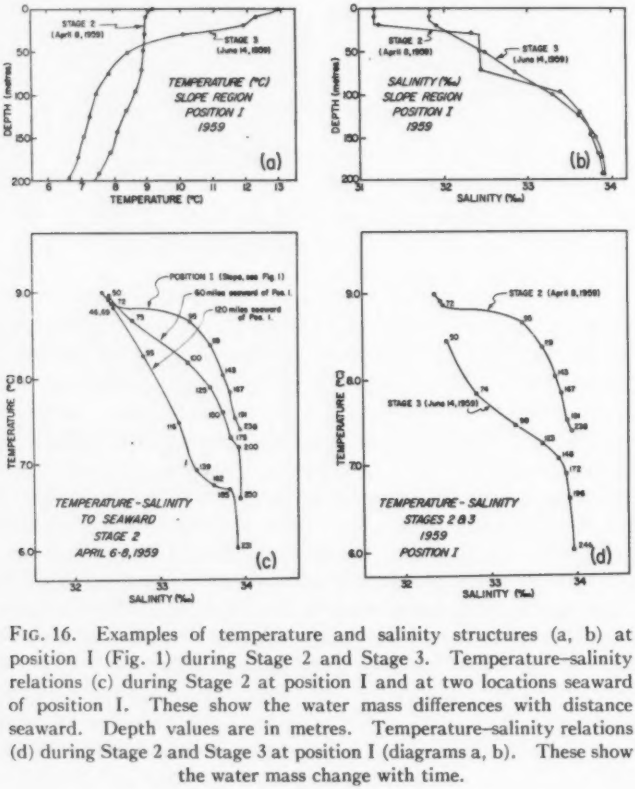

FIG. 16. Examples of temperature and salinity structures (a, b) at position I (Fig. 1) during Stage 2 and Stage 3. Temperature–salinity relations (c) during Stage 2 at position I and at two locations seaward of position I. These show the water mass differences with distance seaward. Depth values are in metres. Temperature–salinity relations (d) during Stage 2 and Stage 3 at position I (diagrams a, b). These show the water mass change with time.

The model of temperature distribution and structure (plots) is shown in Fig. 14b and the structures observed in the several parts of the system are shown in Fig. 15.

When oceanic (OU) water is dominant in the offshore part of the region (Fig. 15a (ii)) the upper temperature zone is 10–20 m deep and the thermocline extends to about 60 m depth. However, if coastal (CU and CH) waters extend beyond the continental slope prior to the development of the temperature structures, these structures are coincident with the salinity structures (Fig. 15a (i)).

In this region at this time there is usually a considerable temperature gradient in the oceanic halocline (Fig. 15a) which constitutes a secondary thermocline (Plot I, Fig. 14b) between 35 and 75 m depth.

It may be recalled that during Stages 1 and 2 the winter wind-induced convergence system was dominant. During Stage 3, that system has relaxed. Coincidentally, there is a marked decrease in the sub-thermocline temperatures in the slope part of the region (Position I) as shown in Fig. 16a, although there is very little change in the salinity (Fig. 16b). This is also shown in the annual cycles of temperature and salinity in Fig. 17. Evidently there is a change of water mass. The temperature–salinity relations at Position I and at two positions to seaward, during Stage 2, are shown in Fig. 16c. The water of a given salinity becomes cooler to seaward. Also water at a given depth becomes cooler and less saline to seaward. These features were also noted by Doe (1955, pp. 10–11). Figure 16d allows comparison of the temperature–salinity relations at Position I during Stages 2 and 3. These confirm that there has been a marked change of temperature at this position during the interval, but little change in salinity. Comparing Fig. 16c and 16d it is evident that the water observed at Position I during Stage 3 is similar to the water found 120 miles to seaward during Stage 2. Evidently this water has moved shoreward during the interval. This movement and the associated rise of the isopleths are believed to be associated with the convergence "relaxation", and/or the beginning of wind-induced divergence during this period.

Over the continental shelf (Plot II, Fig. 14b) the upper zone and shallow (seasonal) thermocline are coincident with the haline CH and CU zones (Fig. 15b). The intensity of the pycnocline inherent in the halocline restricts the downward transfer of heat. As a result the surface waters are usually warmer in the shelf than in the slope and oceanic parts of the section (Fig. 13b (ii)). However, it appears that as this stage develops, the thermal influence on density becomes greater than the haline influence on density and dominates the stability of the composite pycnocline. The decrease in temperature values in the zone below the seasonal thermocline cannot be attributed to surface effects, hence it must be associated with the migration of cooler, deeper water onto the shelf. This was discussed in the preceding section on salinity.

Inshore, the thermal structure is similar to that over the shelf (Plot III, Fig. 14b). The thermocline may extend to near the bottom or it may be more intense in the upper 10–20 m depth (Fig. 15c).

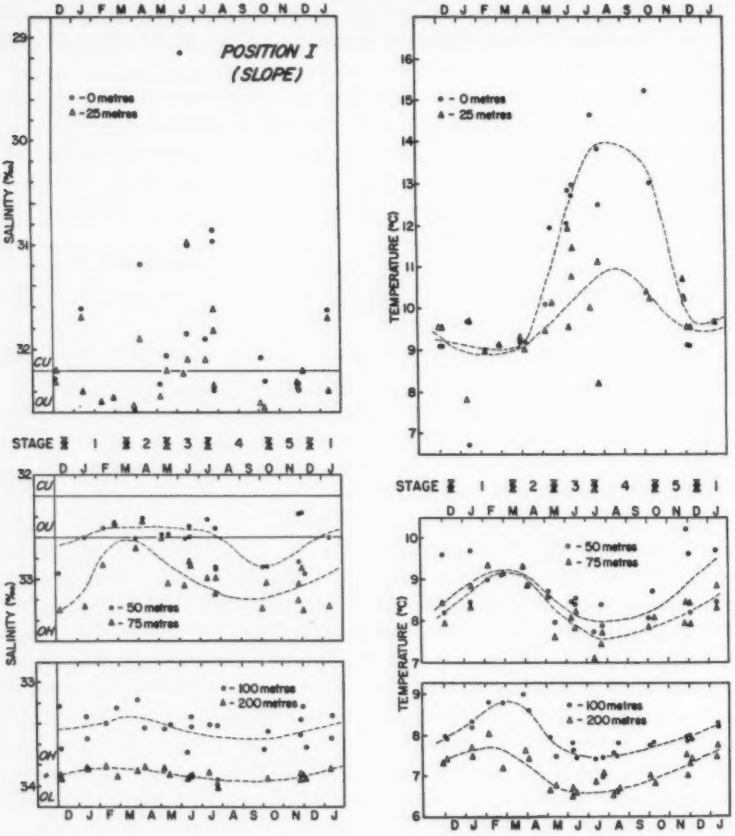

FIG. 17. Temperature and salinity values observed from 1957 through 1961 at position I (see Fig. 1).

STAGE 4 (JULY THROUGH OCTOBER)

During this period, precipitation (Fig. 3a), land drainage from coastal and mainland rivers (Fig. 2) and hence estuarine discharge are low or minimal. Insolation (Fig. 3b) wanes and the rate of heat gain diminishes rapidly. During most of the period the winds are predominantly from the northwest and their strength is less than the annual average (Fig. 5). They induce a dominant weak divergence mechanism. Localized upwelling occurs (Tully, 1942, p. 403; Lane, 1962, p. 72). In October, at the end of the period the occurrence of southeast winds increases so that their frequency is about the same as the northwest winds.

SALINITY. Figure 18a shows an example of observed salinity distribution in the section. Lack of appreciable dilution from land drainage and wind-induced offshore transport of surface water (divergence) result in dissipation of

coastal waters, increased salinity in the upper zone, and weakening of the coastal halocline.

In the oceanic and shelf parts of the region the isohalines are inclined upward toward the coast. They are inclined downward in the inshore part. This is attributed to local effects of estuarine discharge.

The model of salinity distribution and structure (plots) is shown in Fig. 19 and observed structures in the several parts of the section are shown in Fig. 20.

During this period the occurrence of distinctive coastal (CU and CH) water beyond the shelf is rare. The oceanic structure (Plot I) contains a shallow (20 m) upper zone (OU), a halocline extending to about 150 m depth, and a lower zone.

The shallowness of the upper zone (OU) is attributed to the divergence situation which dissipates the surface water seaward, and induces uprising of the deeper waters. Because the winds are not steady these conditions are variable. Their correlation with the wind cannot be estimated at the present time, because the lag of the sea after the wind is not known.

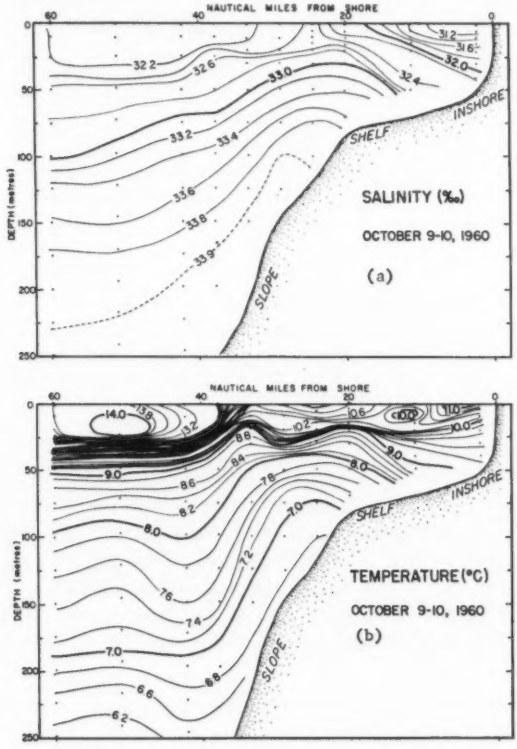

FIG. 18. Examples of salinity and temperature structure, Stage 4.

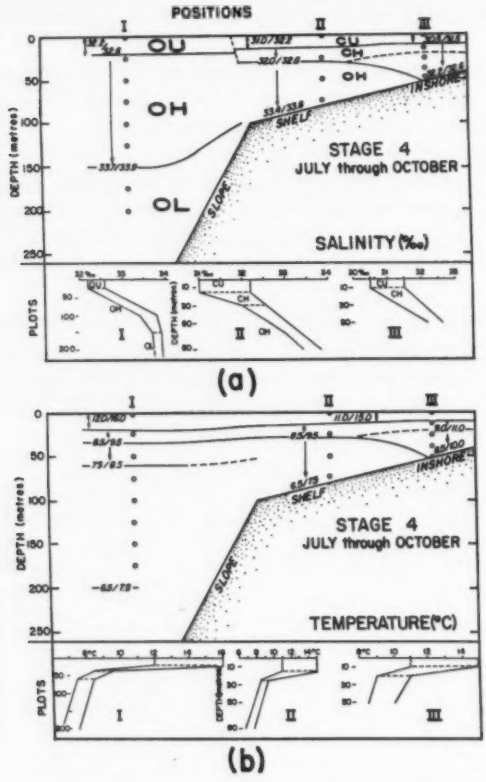

FIG. 19. Model of structure and distribution in a vertical plane seaward of Amphitrite Point, B.C. (Fig. 1) and *plots* of structures showing ranges of values at positions I, II and III (Fig. 1). (a) Salinity, Stage 4. (b) Temperature, Stage 4.

Over the continental shelf (Plot II, Fig. 19) the coastal upper zone (CU) is about 15 m deep (Fig. 20b). Below it the coastal halocline (CH) extends to 20–30 m depth. Oceanic upper zone (OU) water does not occur over the shelf at this time. Rather, the oceanic halocline (OH) exists below the coasta halocline (CH) water. Frequently the demarcation becomes indistinct as indicated by the ranges of salinity values and the structures (Fig. 20b). In these cases the halocline is very nearly continuous through the CH and OH zones (Plot II, Fig. 19a).

Inshore (Plot III, Fig. 19a) the upper zone (CU) is about 10 m deep. Although oceanic halocline (OH) water may penetrate this far inshore, below 30 m depth, the general case shows that the coastal halocline (CH) is continuous to the bottom, with an intensification in its upper portion.

It is observed that the isohalines are inclined downward toward the shore in the shelf and inshore parts of the section. The crest of the isohalines occurs over the outer shelf. It is reasoned that the upward inclination would be continuous to the surface or the shore, as they are off the California coast (Sverdrup *et al.*, 1942, pp. 500–502) if part of the demand for divergence water were not provided by estuarine discharge. In California there is virtually no land drainage in summer, and the northwest Trade Winds predominate. The divergence situation becomes fully developed and creates a demand for replacement water along the coast which can only be satisfied by upwelling from the depths (Sverdrup *et al.*, 1942, p. 725). Northward from the Columbia River there is considerable estuarine discharge, even during this "dry" season. Also the winds are variable, although they are predominantly from the northwest. Hence the divergence situation is rarely, if ever, fully developed, and part of the demand for replacement water is met by estuarine discharge. It is reasoned that the crest of the inclined isohalines marks the division between the shoreward part of the section where

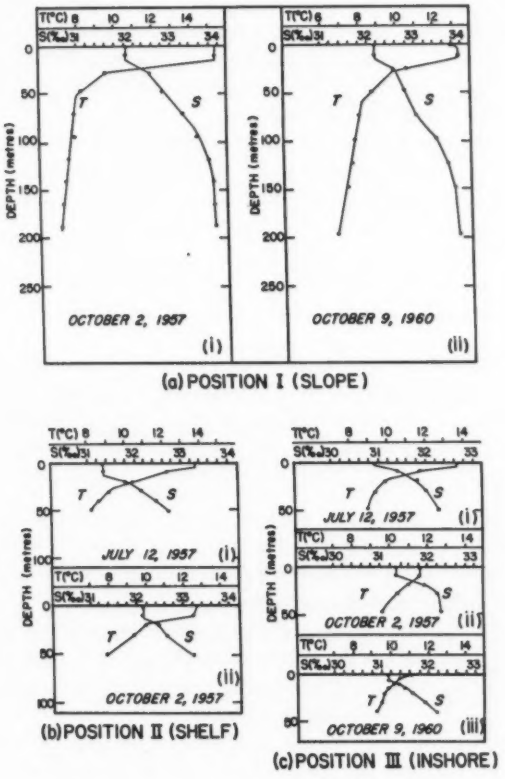

FIG. 20. Examples of data during Stage 4 (Fig. 19).

the demand is met by estuarine discharge, and the seaward part where the major contribution is from the underlying waters.

TEMPERATURE. Figure 18b shows an example of observed temperature distribution in the section. The surface temperature increases from the shore to a maximum seaward of the continental slope. The seasonal thermocline is continuous and increases in magnitude to seaward. Below this there is considerable temperature structure in which gradient and the inclination of the isotherms are coincident with the haline structure.

The model of temperature distribution and structure (plots) is shown in Fig. 19b and the observed structures in the several parts of the section are shown in Fig. 20.

The waters are warmest (12 to 16° C) in the offshore upper zone which extends to about 20 m depth (Fig. 18b). In the oceanic and slope part of the section, the seasonal thermocline occurs in two segments (Plot I, Fig. 19 and 20a). The more intense thermocline extends to 35 m, about the same as during Stage 3. This shallow thermocline is not as intense in the shelf region because of the movement of surface-warmed waters seaward. The deeper thermocline is more intense than in Stage 3 due to the divergence mechanism at the edge of the slope region. Over the shelf, it blends with the lower halocline and is continuous to the bottom, due to the rise of isotherms onto the shelf from the sub-thermocline oceanic water (see Fig. 6—divergence).

Over the shelf, the bottom of the upper thermocline extends to about 30 m depth early in this Stage (July). Later (October) it rises to about 20 m depth (compare Fig. 20b (i) and b (ii)). This rise is believed to indicate an increase of divergence between the periods of observation.

Inshore, the 11 to 15° C upper zone is about 10 m deep (Fig. 20c) or non-existent. The thermocline coincides with the halocline with occasional intensification in the upper 20 m depth (Plot III, Fig. 19b).

STAGE 5 (OCTOBER THROUGH DECEMBER)

During this period runoff from the mainland sources is small (Fig. 2b) but the period of increased runoff from local estuaries (Fig. 2a) is associated with the maximum coastal precipitation (Fig. 3a). The winds are predominantly southeast and of moderate intensity (Fig. 5).

SALINITY. Two examples of salinity structure in the section are shown in Fig. 21a (i) and (ii). In general the near-surface salinity increases to seaward in an isohaline upper zone. Below this there is moderate structure. In one set of data the isohalines are inclined slightly downward to the coast in all parts of the section. In the other they are slightly peaked over the outer limit of the continental shelf, reminiscent of the Stage 4 structure, but much less marked. Evidently the oceanographic mechanism is alternating between divergence and convergence, neither becoming fully developed.

The model of salinity distribution and structure (plots) is shown in Fig. 22a and some examples of observed structure in the several parts of the section are shown in Fig. 23.

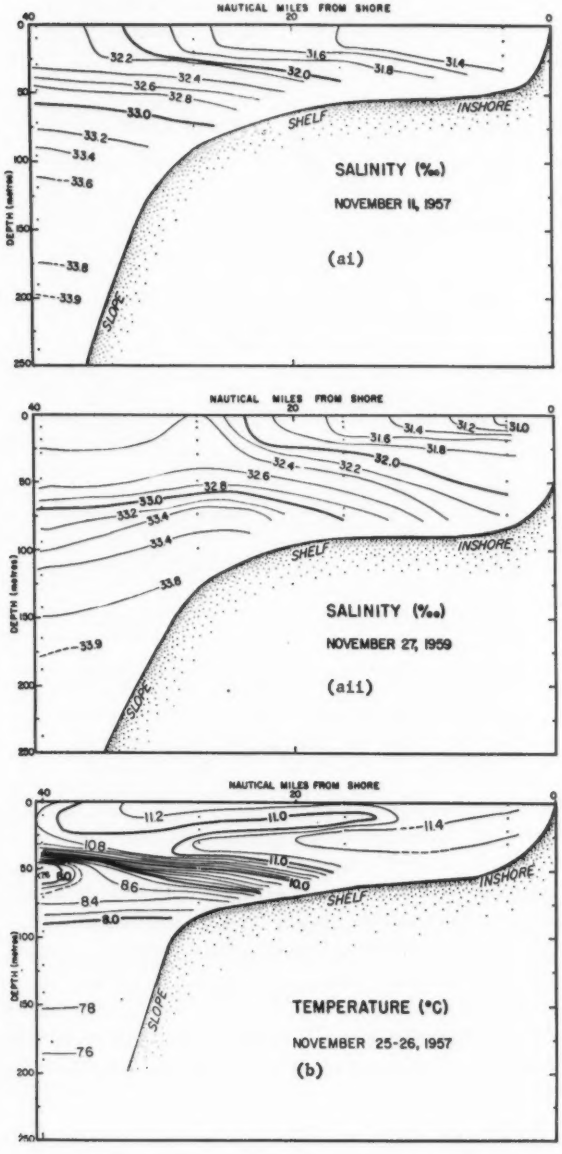

FIG. 21. Examples of salinity and temperature structure, Stage 5.

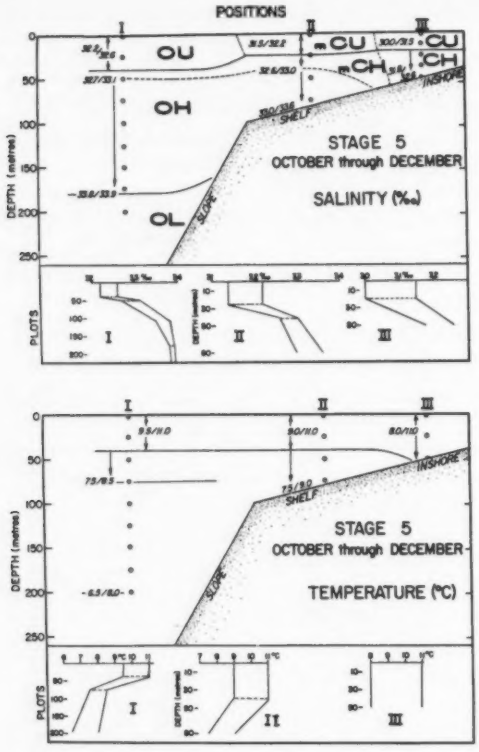

FIG. 22. Model of structure and distribution in a vertical plane seaward of Amphitrite Point, B.C. (Fig. 1) and *plots* of structures showing ranges of values at positions I, II and III (Fig. 1). (a) Salinity, Stage 5. (b) Temperature, Stage 5.

During this stage the oceanic upper zone (OU) deepens to about 40 m (Plot I, Fig. 22a and 23a). This results in an intensification of the top of the oceanic halocline (OH). Its base descends to about 180 m due to the advent of convergence.

In the shelf part of the region (Plot II, Fig. 22a and 23b) the coastal upper zone (CU) becomes 20–30 m deep. It may or may not cover the whole shelf but never extends into the slope part of the section. It is slightly more saline than during Stage 4, probably due to deeper mixing. The halocline lies between 25 and 35 m depth.

Inshore (Plot III, Fig. 22a and 23c) the coastal upper zone (CU) is 10 to 30 m deep, and below it the halocline (CH) extends to the bottom.

TEMPERATURE. During this period, insolation decreases (Fig. 3b) and cooling becomes the dominant process in the heat budget. The thermocline

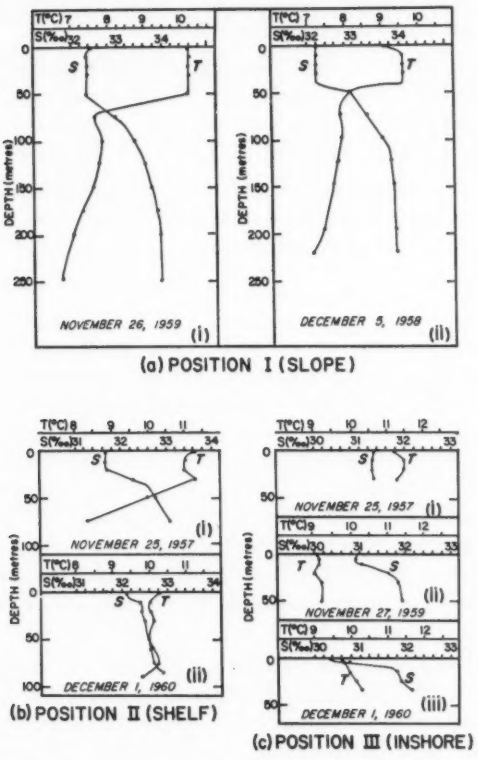

FIG. 23. Examples of data during Stage 5 (Fig. 22).

decays, sinks and is compressed as heat is lost from the sea surface. Surface waters become colder than the underlying waters, and convective sinking (and mixing) occurs unless prevented by haline stability.

Figure 21b shows an example of temperature structure in the section during this stage. There is a deep upper zone with evidence of large temperature inversions, although stability is maintained by the salinity structure. Below this, there is an intense thermocline, slightly inclined toward the continental shelf.

The model of temperature distribution and structure is shown in Fig. 22b and examples of observed structure in the several parts of the section are shown in Fig. 23.

In the offshore part there is an isothermal zone, coincident with the salinity upper zone (OU), to about 40 m depth. In this zone small temperature inversions near the surface are common. The decaying thermocline extends down to about 75 m depth. The deepening of the base of the thermocline, and the slightly warmer temperatures at 200 m, compared to Stage 4, signify the relaxation of the

summer divergence condition. This is confirmed by the increase of temperatures in the sub-halocline water shown in Fig. 17.

Over the shelf (Plot II, Fig. 22b; Fig. 23b), the isothermal layer may be deeper than the haline upper zone (CU). This suggests that the source waters have similar temperatures at this time, or that the surface waters have been cooled to the same temperature as the waters in the halocline.

A variety of temperature structures may be found next to the coast. Depending on the relative influences of wind, surface cooling, and the temperatures of the estuarine and oceanic waters, the structure may be negative, isothermal, or positive.

SUMMARY

It has been shown that the waters over the continental shelf and slope, west of Vancouver Island, contain structural features which can be related to general meteorological conditions. On the basis of seasonal climate, the observed changes in structure have been used to define five main divisions or stages in the chain of oceanographic events. Although it has been shown that short-term variability is considerable, the large scale characteristics of each stage are intended to provide a basis for research on a finer scale. As it stands, the model with its relatively large, yet definitive, ranges of values for the basic properties may prove to be of value to workers interested in just such ranges (e.g. fisheries biologists).

It is of interest to note that Pickard (personal communication) has found a relationship between the maximum densities throughout the near-shore vertical column (taken from the ranges given in this model) and the maximum densities found in the west coast of Vancouver Island inlets. His plot of inlet density maxima versus sill-depth contains values which are less than or almost equal to those contained in the plot of the maximum densities versus depth for the coastal region. He postulates that the inlets serve as a "memory" of maximum near-shore densities and concludes that the extreme values suggested by this model "... are probably typical of long term conditions".

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The Effect of Tagging with Petersen Disc Tags on the Swimming Ability of Fingerling Steelhead Trout (*Salmo gairdneri*)[1,2]

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ABSTRACT

Fingerling steelhead trout were given individual performance tests in an experimental flume. Barriers confined the fish to a 10-foot (1 foot = 30.48 cm) testing section where they swam against a constant velocity of 2.5 feet per second. The end point of each test was reached when the fish was fatigued enough to allow itself to be impinged by the water flow on a net barrier. The study was designed to test what effect the application of Petersen disc tags had on swimming endurance, by comparing tagged, handled, and control groups.

No permanent reduction of swimming endurance was experienced by the handled group (tag pin inserted, then removed). The tagged group experienced a permanent drop of about 50% in their swimming endurance due to the presence of the tag.

INTRODUCTION

It is generally recognized that fish offer very little resistance to the water when swimming. Gray (1953) discusses the paradox, that if the resistance of a fish was the same as a most carefully built model towed through the water, then it can be calculated, using applicable engineering formulae, that the fish could not possibly swim as rapidly or maintain itself in currents for as long as it does. Thus, an actively swimming fish must be able, by nature of its movements, to lower its resistance to the water. If this is the case, then any additional drag such as a tag, might well weigh heavily on the fish's endurance at a given velocity.

It is easily observed that the leading edges of a loosely applied disc tag will be forced out in a water flow and appear to offer considerable resistance. Alverson and Chenoweth (1951) looked into the resistance of this tag in an ingenious way. They found that returns were lacking from albacore tagged with the Petersen disc tag and had reason to believe, since albacore are such extremely rapid swimmers, that the tag was actually being pulled out due to its hydraulic resistance. They tested frozen albacore in a "water tunnel" and found that at water velocities of 18–22 mph (26–32 fps) 14.5-mm (diameter) Petersen disc tags applied below the dorsal fin were forcibly pulled out of the flesh in a matter of minutes.

The above work would suggest that the tag is offering considerable resistance to the water when applied to a frozen fish. If live fish are not able to overcome

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it, then tagged salmon might have to expend a greater amount of energy on a long trip upstream and exhaust their energy stores before they can effectively spawn. Perhaps these tagged fish could be blocked by areas of high velocity while their untagged counterparts would be able to pass through. The present study was undertaken to evaluate the possibility that deterioration in swimming ability may follow the application of Petersen disc tags to young steelhead trout, and if such a deterioration could be demonstrated, to determine its cause.

MATERIALS AND METHODS

This experiment was designed to compare daily performances of tagged, handled (tag pin inserted and removed), and control groups. To insure that similar fish would be assigned different treatments, the fish were tested for several days before tagging or handling to establish their performance levels.

It was hoped that the results of the experiment would determine whether: (1) immediate effects of handling resulted in an appreciable reduction in performance level; (2) the handled fish experienced a persistent reduction in performance level; (3) the presence of a tag would result in a persistent reduction in performance level.

Description of Apparatus

The performance experiments were conducted in a 24½-ft straight flume, constructed in the summer of 1959 under a Navy contract (Kent *et al.*, MS, 1959). The flume was 2 ft deep, 14 inches wide, and except for a 6-ft plexiglas "observation section" in the middle, was constructed entirely of ¾-inch fir plywood. The flume operated as a recirculating system. Pumps delivered water from an 11,000 gallon sump into a 1500 gallon main head box. The water then flowed through a connecting duct, into the flume head-box, through a series of baffles, and into the flume. Four openings in the rear end of the flume spilled the water back into the sump.

The temperature of the water in the system was controlled. Operation of the flume warmed the water slowly, depending on the room temperature. Refrigeration coils in the sump were used to cool the water or counteract operational warming. During the experiment, the temperature in the flume was held within one-third of a degree F from that in the fish holding compartments.

Experimental Subjects

Fingerling *Salmo gairdneri*, about 6 inches in length, were chosen as experimental subjects. These fingerlings were raised in the College of Fisheries Experimental Hatchery from spawn taken in April 1959 from adult steelhead that were returning to the hatchery fish-ladder.

There were many advantages to using small fish: (1) holding the fish individually was simplified since hatchery troughs could be easily partitioned for the purpose; (2) several thousand fish were available and a group having nearly the same length could be selected; (3) since the fish were immature, sexual differences should be non-existent; (4) effects of tagging and handling were magnified; (5) basic questions pertaining to handling and tagging could be answered.

Barrier Selection

Paulik and DeLacy (1958) utilized an *electrode barrier* in their work with adult salmon in a 25-ft flume. The barrier consisted of spring steel electrodes spaced across the channel, each electrode bearing the opposite charge of its neighbor. The swimming fish was stimulated when his tail entered the electrical field.

Fields *et al.* (1954) used an *impingement barrier* in their work on fingerling silver salmon in another flume. This barrier consisted of a screen fixed across the channel at right angles to the direction of water flow, and the fish was stimulated by his natural behavior of avoiding impingement.

Preliminary experiments indicated three distinct advantages to the use of an impingement as opposed to an electrode barrier: (1) the amount of stimulation a fish derives from electrodes is dependent upon the manner in which it encounters them, while the motivation supplied by a fixed net does not vary; (2) fish cannot reverse direction and pass through a net barrier; (3) the fish is not harmed by impingement on a net barrier. Exploratory tests also indicated that more consistent and reliable performance figures could be obtained using the net barrier.

The impingement barrier was constructed of $\frac{1}{2}$-inch mesh, and an upstream net of $\frac{3}{4}$-inch mesh gill net was installed so that the two nets enclosed a 10-ft section of the flume. Since fingerlings have been observed to avoid bright lights (Fields, 1954), two 150-watt waterproof spotlights were installed immediately behind the impingement net, shining diagonally through the net and focusing on the bottom of the channel just in front of the net. A 150-watt spotlight was also placed above the upstream net and aimed at the net in such a way that the net and the area immediately downstream of the net were brightly illuminated. The room was darkened during performance tests, and generally the fish swam between the two light sources until exhausted (Fig. 1).

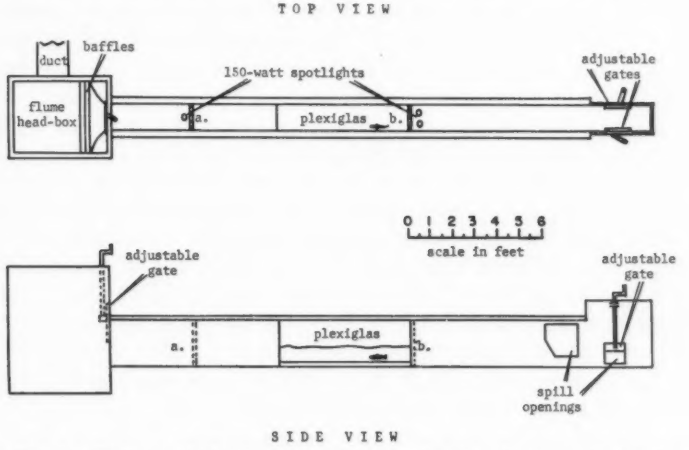

Fig. 1. Diagram of the experimental flume showing the upstream barrier net (a), and impingement net (b).

Velocity Pattern

Fields *et al.* (1954) and Calkins (1959) reported that fingerlings would seek out low-velocity areas such as standing waves and corners of the flume if available, and swim in these areas. It was thus necessary to obtain an even velocity pattern over the whole 10-ft experimental section. To eliminate the corners where the sides met the bottom, 10-ft wooden inserts of a triangular cross-section were installed. The apparatus was carefully adjusted to provide the fish with a constant velocity of 2.5 fps.

Swimming Behavior

It was readily noticed that while most of the fish were erratic swimmers on the first day they were tested, they apparently soon became accustomed to the apparatus and swam almost entirely in the lowest velocity areas (bottom, face of triangular boards, or along the lower sides of the channel). While only 5 out of the 36 could be considered steady swimmers on the first test day, 14 out of the 36 were considered steady on the second day, 25 out of the 36 on the third day, and 30 out of the 36 on the fourth. After regressing slightly on the fifth day (when handling took place), the latter ratio was maintained for the rest of the experiment.

Holding Facilities

The fish were held in two concrete hatchery rearing troughs, 11½ inches wide, and 15 ft long. Each trough was divided into 18 individual compartments, each about 9 inches long, by stainless steel perforated dividers that were held in place by rubber gaskets. Framed screens covered with brown translucent paper were used to cover the troughs.

Experimental Procedure

It was necessary to have some means of transporting the fish from the holding compartment to the flume without the fish becoming excited or exhausted. Experimentation showed a 14-ounce jar covered with black plastic tape to be very satisfactory. A ⅜-inch wide slit was cut in the tape extending the length of the jar, and the bottom of the jar was left uncovered. The jar was carried with the slit uppermost which enabled the experimenter to observe the actions of the fish while it was being carried to the flume. The fish would quite readily swim into the jar when the open mouth was offered them, and the "twist-off" cap allowed for easy opening and closing of the bottle Very few fish struggled and they all oriented themselves facing the clear bottom of the bottle. This orientation was very helpful and made possible consistent introduction of the fish into the flume. The fish were introduced about 7 ft upstream of the impingement net to give the introduced fish sufficient time to orient themselves and begin swimming before encountering the net. The fish were introduced into the flow with their heads pointing downstream, since preliminary tests indicated that this was the preferred orientation.

The carrying bottle worked very satisfactorily. The fish were easily captured and although 11 of the 36 fish struggled in the bottle on the first day,

never more than two out of the 36 struggled on any succeeding day. The slight struggling observed in these later instances was not considered sufficient to cause any decrease in performance.

The introduction of the fish into the flume was also very satisfactory. Out of over 300 introductions, in only 12 instances did fish not immediately begin to swim, and nine of these immediate impingements occurred on the first three test days. These impinged fish were promptly helped off the net if they did not swim off by themselves.

Ideally then, the fish would swim between the two lighted areas until exhausted. As a fish tired, it was carried closer to the downstream net. Contact with the net would often stimulate the fish to swim a short time longer, at the end of which it would struggle on the net, then become impinged. A fish was considered impinged if it was held motionless on the net by the water flow for at least one second.

When the impinged fish ceased struggling, it was allowed 10 seconds, and if no movement occurred, this was considered the end point. The experimenter then gently scooped the fish off the net with his hand, placed it in the carrying bottle, and returned it to its holding compartment. If the fish swam off the net or renewed its struggling when capture was attempted, it was released, a second stop watch started, and a new end point reached.

The gross timing of the test was corrected by the use of a third stop watch which was non-zeroing and was allowed to run whenever the fish was lying motionless on the net. By subtracting this timing from the gross timing, a corrected timing was obtained which was the actual total time the fish spent swimming or struggling on the net. This was the measure of swimming ability used for comparison.

Tagging and Handling Procedures

To simulate field conditions, the fingerlings were dip-netted from their compartments and tagged in a miniature tagging cradle. A flap of black rubber at one end of the cradle covered the fish's head and reduced its struggling. No anesthetic was used since it was felt that this would add another variable to the experiment.

The experiment was designed to compare performances of tagged, handled, and control fish. The tagged group was tagged with $\frac{1}{2}$-inch disc tags while the handled group underwent similar handling, but the tag pin was merely inserted, then removed. The performances of the tagged fish before, immediately after, and for several days after handling could then be compared with the handled and control fish.

Since exploratory tests indicated that loosely tagged fish might be impaired in their swimming to a greater extent than tightly tagged ones, it was necessary to devise an instrument that would measure the looseness of an applied tag. Inside calipers were constructed of two plexiglas tubes, one sliding inside the other. A scale on the outer tube provided a measure in millimeters of the tag looseness.

On the basis of exploratory tests, 3–4 mm of looseness was selected for tagging. To provide this amount of looseness to the applied tags, an $\frac{1}{8}$-inch diameter glass tube 18 mm long was slipped on the tag pin after the second disc had been applied, and the pin was then clipped off flush with the top of the tube. The tube was then removed and a single loop "knot" was applied, resulting in most cases in the desired amount of tag looseness. The tags were applied below the insertion of the dorsal fin with 2-inch tag pins made of .036-inch soft nickel wire.

At the conclusion of the experiment, the looseness of the tags to the nearest millimeter was measured immediately after each fish was tested. These measurements showed that only three out of the 10 tagged fish had more than 4 mm of tag looseness, the remaining seven fish had 3–4 mm of tag looseness.

Testing Procedure

Each of the 36 fingerlings was tested once each day for four days. On the basis of those tests, the fish were matched in triplets so that all three fish of each triplet performed at nearly the same level. Six fish were eliminated from the design because they were either poor swimmers or could not be matched with fish of comparable performance in a triplet. The members of each triplet were randomly assigned a treatment (tagged, handled, or control). This method of assignment not only enabled a comparison of similar fish undergoing different treatments, but also assured a uniform dispersion of treatments. Immediately after each fish underwent its assigned treatment, it was subjected to a performance test to determine immediate effects. The fish were then tested once a day for five more days to establish a reliable comparison.

Since it was felt that feeding during the experimental period would more than likely induce variability into the data, the fish were not fed from 48 hours before the first test, until the end of the experiment.

The fish were tested in the same order each day. The compartments were numbered consecutively from the base to the head of each trough. The fish were randomly assigned to the compartments and tested in numerical order. Thus the fish "just tested" was always returned "downstream" of the next fish to be tested.

RESULTS

The 30 fish (148–156 mm total length) selected for this experiment were tested once each day for 10 days for a total of 300 individual performance tests (Table I). The mean and individual daily performances are presented in Fig. 2. The following general trend is shown by the control means: increasing performances for the first four days, a rather sharp decline on days 5 and 6, and a rather steady performance level for the remaining four days. This general trend also appears evident in the handled and tagged group means. Another apparent trend is the reduction of the variance around the means toward the last of the testing period.

TABLE I. Results of the December 12, 1959 experiment using fingerling steelhead tested in the 24½-ft straight flume (C = control; H = handled; T = tagged).

Fish No.	Treatment	Tag looseness (mm)	Daily performances in seconds									
			1	2	3	4	5	6	7	8	9	10
1	H		273	541	485	591	215	433	453	444	422	352
2	C		550	621	611	1064	588	604	527	485	514	462
3	C		587	554	589	663	547	491	450	430	428	405
5	T	3	635	649	555	769	126	273	288	292	257	185
6	C		385	405	422	490	462	400	409	407	342	410
7	H		493	569	697	814	108	518	523	525	533	440
8	T	5	572	477	587	783	36	169	151	164	195	174
9	C		627	697	631	837	641	591	576	490	489	371
10	C		436	490	563	594	580	495	454	491	436	416
11	T	3	409	472	623	690	79	180	170	177	184	144
12	T	8	565	426	132	347	55	35	78	172	90	111
14	H		434	537	585	578	358	530	490	437	401	456
17	H		490	560	273	537	211	399	413	434	482	385
18	H		336	347	385	461	199	407	388	415	403	387
19	H		337	458	511	681	365	327	448	387	429	450
20	C		672	617	763	848	568	408	481	461	438	415
21	T	5	624	670	584	635	18	179	139	147	137	187
23	T	4	393	488	489	601	102	221	208	197	203	215
24	H		597	578	724	712	299	538	435	465	458	451
25	T	4	708	839	619	1059	154	277	233	231	204	169
27	H		378	425	389	375	181	405	378	323	319	320
28	C		275	404	491	635	527	403	254	344	404	376
29	T	4	553	522	573	606	51	255	238	223	169	231
30	H		533	534	852	1168	141	608	549	550	552	478
31	C		517	646	553	555	384	358	362	354	425	334
32	T	4	308	425	463	488	28	178	162	174	123	148
33	C		57	360	445	382	214	146	232	302	318	314
34	H		66	593	576	633	260	508	535	614	538	440
35	C		767	427	242	563	389	243	337	308	375	405
36	T	3	496	468	411	384	78	184	110	208	227	221

A comparison of the mean performances of the control, handled, and tagged groups on test day 5 shows that the mean performance of the group that was handled but not tagged dropped significantly when compared to controls (t = 5.23, $P<0.01$), and the tagged group experienced an additional drop of performance to such an extent that it was significantly different from the mean performance of the handled group (t = 5.26, $P<0.01$).

An examination of the mean performances of the different groups on days 6 through 10 shows a small difference between the control and handled means (not statistically significant at 5% level). The mean performances of the tagged group, however, are seen to be consistently much lower than those of the control

group. This difference was shown to be highly significant by means of an analysis of variance test, performed using the individual performance data ($F = 216$, $P < 0.01$).

In order to enable a visual comparison between individual triplets, Fig. 3 was constructed. The triplets have been arranged in order of their average performance level. It is apparent that the same general picture is shown as was seen by comparing the means.

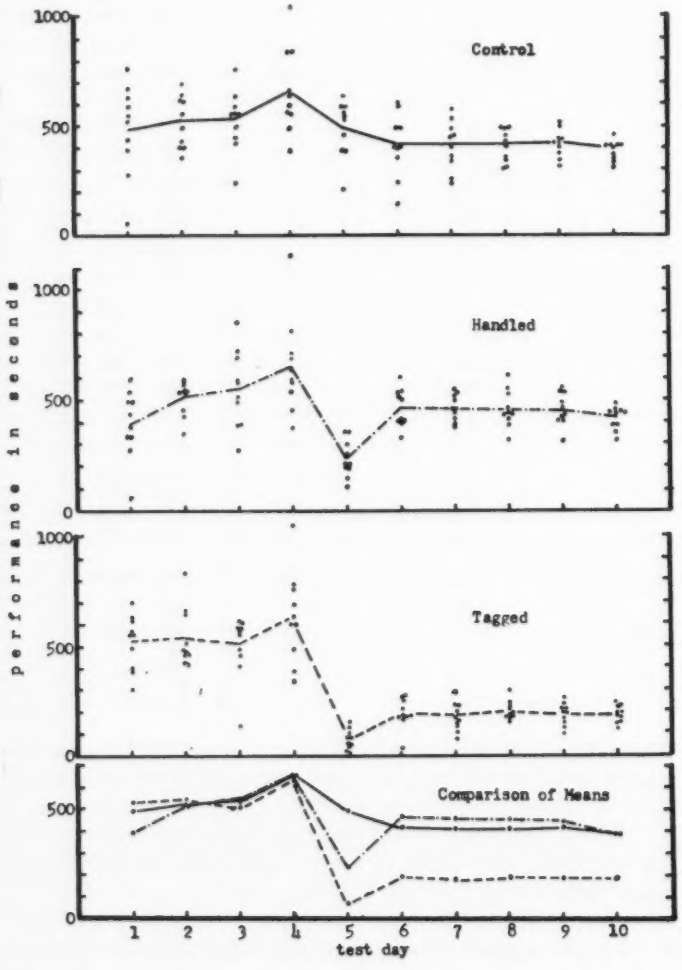

FIG. 2. Individual and mean performances of the 30 fingerling steelhead.

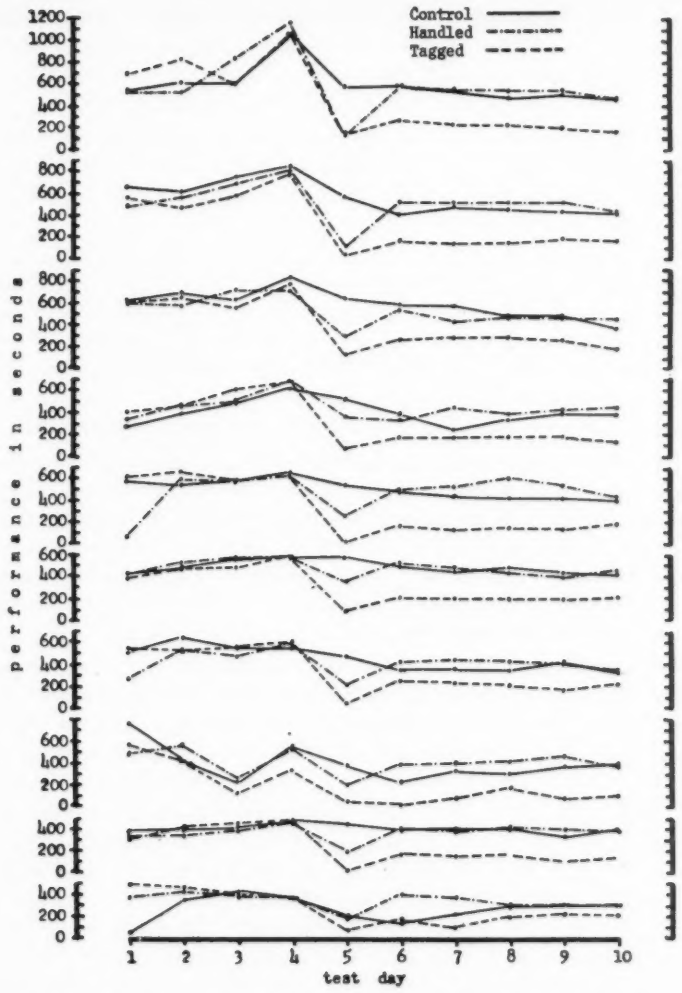

FIG. 3. Performance comparison for the 10 matched fingerling steelhead triplets.

DISCUSSION

This experiment demonstrated quite conclusively that the application of Petersen disc tags can markedly reduce the swimming ability of the tagged fish. Fish tested immediately after tagging showed a drop of 85% in length of time they could swim as compared to controls. Testing handled fish immediately after handling showed a drop of 52% in performance as compared to controls. When the handled fish were retested 24 hours later, it was found that their

performance had recovered to the control level, and this level was maintained throughout the rest of the experimental period. Tagged fish, however, did not show a complete recovery, and their average performance throughout the remainder of the experiment was only 46% of the control's average.

Thus the presence of a disc tag can cause a significant decrease in the swimming ability of fish. That this decrease is due to the presence of the tag and not the shock or injury of handling was demonstrated by the complete recovery of the handled group.

Although the experiment was not designed to establish the exact relationship between tag looseness and performance, an examination of the data for test days 6 through 10 does indicate a relationship. In order to make the performances of the tagged fish comparable, for each triplet the tagged fish's performance was averaged and shown as a percent of the average of the combined performances of the control and handled members. The limited data when plotted does indicate that the more loosely tagged fish gave the lower performances (Fig. 3).

Thus, tagging experiments using Petersen disc tags should be designed to utilize the smallest diameter disc that is practical. Also, mature non-growing fish (such as migrating adult salmonids) should be tagged tightly to reduce the hydraulic drag. The presence of the tag pin in the muscle masses may have had a contributing depreciatory effect on endurance, resulting from either physical interference or irritation. The extent of these effects could provide a subject for further experimentation.

It was shown that the fish were considerably fatigued by the handling involved in the tagging operation. Therefore, experiments should be designed to fatigue the fish as little as possible in tagging operations and if feasible allow the fish an area where it can recover from fatigue before it confronts high velocity flows or predators.

The general changes in the mean performance level of the control group during the experiment, merit discussion. The average performance increased during the first four days of testing, then declined on the fifth and sixth days. Since the fish were not fed during the experimental period, it is possible that this decline might have been due to the depletion of an energy source. However, since this decline ended on the sixth day and a nearly level or very slightly declining average performance level was observed throughout the remainder of the experiment, it appears that the fish were able to draw on some other energy source, probably fat stores, to sustain themselves at this reduced performance level.

In conclusion, this study has shown the straight flume, combined with impingement as a criterion of fatigue, to be an extremely valuable apparatus for performing basic and applied research on the swimming ability of fish. Thus, with the advent of means to measure a fish's normal swimming performance it becomes possible to determine the effect of modifying a fish physically or physiologically by measuring changes in the fish's performance level. Much research needs to be done in this almost virgin field.

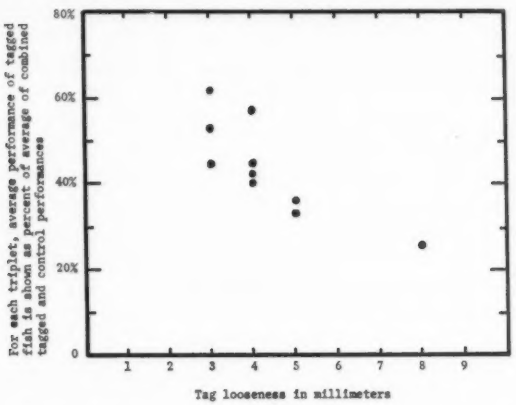

FIG. 4. Relationship between performance of the tagged fish and the looseness of the tag. (To facilitate comparability of the triplets, the performance of each tagged fish is shown as percent of the average of the pooled, control, and handled fish performances.)

SUMMARY

1. Thirty-six fingerling steelhead (about 6 inches in length) of hatchery stock, were given daily individual performance tests in a hydraulic flume at the College of Fisheries, University of Washington, using impingement on a stationary net as the criterion of fatigue. On the basis of their individual performances on the first four days, 30 of the fish were matched in triplets. The members of each triplet were randomly assigned as either tagged, handled, or control fish and treated on the next day. Each fish was tested immediately after treatment, and was then tested for five more days for a total of 10 test days resulting in 300 performance tests.
2. The average performance of the control group was observed to rise for the first four days, decline on test days 4 and 5, then remain at a rather constant level for the remaining five test days.
3. To determine how completely exhausted the fish were by the handling procedure, the handled fish were tested immediately after handling. A comparison of the handled and control means indicated about a 50% drop in performance due to fatigue caused by handling. Within 24 hours, however, the handled fish had recovered their performances which were then indistinguishable from those of the controls.
4. Testing tagged individuals after they had recovered from the fatigue of the operation, showed a permanent 46% reduction in the length of time they could swim in the apparatus. The complete recovery of the handled group indicates that this loss in swimming ability of the tagged group was due to the presence of the tag.

ACKNOWLEDGMENTS

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Source of Paralytic Shellfish Toxin in the Bay of Fundy[1]

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ABSTRACT

Seasonal rise in shellfish toxicity in the Bay of Fundy in 1961 was coincident with increased abundance of a marine dinoflagellate, *Gonyaulax tamarensis*, and the appearance of toxin in plankton extracts. Experiments with unialgal cultures of *G. tamarensis* isolated from the Bay of Fundy provided overwhelming evidence that it is the primary source of toxin in shellfish in this area and the Gulf of St. Lawrence. *G. tamarensis* is widely distributed in the North Atlantic and there is evidence of toxic and non-toxic strains of this species.

INTRODUCTION

Accumulation of paralytic toxin in molluscan shellfish in the Bay of Fundy and the estuary of the St. Lawrence on the Atlantic coast of Canada is a seasonal phenomenon. Since human illnesses and fatalities have resulted following ingestion of affected shellfish from these areas, much concern has been aroused among public health and fisheries agencies. Several studies have been carried out to understand the poison problem and to discover the primary source of shellfish poison in this area (Sullivan, 1946; Medcof *et al.*, 1947; Needler, 1949; Bond and Medcof, 1958, and Medcof, 1960). But it was not until 1961 that an investigator was assigned to this investigation full time by the Fisheries Research Board of Canada, and a comprehensive program of field and laboratory investigations was developed. The purpose of the present study has been to provide the information that will be needed eventually to design a more efficient system of monitoring and predicting danger periods. The Board's work has since centred in the Bay of Fundy and has prospered through active collaboration with the Department of Fisheries of Canada and the Department of National Health and Welfare.

Analysis of 15 years' toxicity records in relation to hydrographic and meteorological factors (Prakash and Medcof, 1962; Prakash, 1962) gave direction to the current phases of our research program. This has involved tracing the poison in shellfish to its source and a re-examination of the relative importance of the various environmental factors that regulate annual build-up and fall-off of shellfish toxicity levels in particular areas.

For years there has been circumstantial evidence that molluscan shellfish derive their toxin from feeding on planktonic dinoflagellates. In their studies of paralytic shellfish poison on the Pacific coast of the United States, Sommer *et al.* (1937) suggested certain species of the genus *Gonyaulax* as the source of

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shellfish poison. Commenting on the European outbreaks, they pointed out the possibility of a brackish water form like *Gonyaulax tamarensis* being the causative organism in the North Sea. Medcof *et al.* (1947) indicated a parallel seasonal rise in shellfish toxicity and the abundance of *G. tamarensis* in the Bay of Fundy. Needler (1949) examined the plankton from Head Harbour in the Bay of Fundy from 1944 to 1947 and indicated a quantitative relationship between rise in shellfish toxicity and the abundance of *G. tamarensis*.

Although these earlier studies provided useful information and guidance, a reliable identification and proof of the source of shellfish poison were still lacking. After opening our investigations in 1961, it became clear that a definite recognition and isolation of the causative organism was an essential prerequisite to further work on shellfish toxicity. The present paper reviews toxicity trends in the Bay of Fundy in 1961 and deals with field and laboratory attempts to isolate and identify the organism responsible for shellfish poison.

FEATURES OF 1961 TOXICITY

Moderately high toxicity scores were recorded in 1961 on the New Brunswick as well as on the Nova Scotia side of the Bay of Fundy and at least six persons were taken ill due to consumption of poisonous shellfish. Toxin titres started building up in most areas from the second week of June when surface water temperature was around 7° C. However, peak scores were not recorded until late July and early August when surface water temperature was well over 10° C.

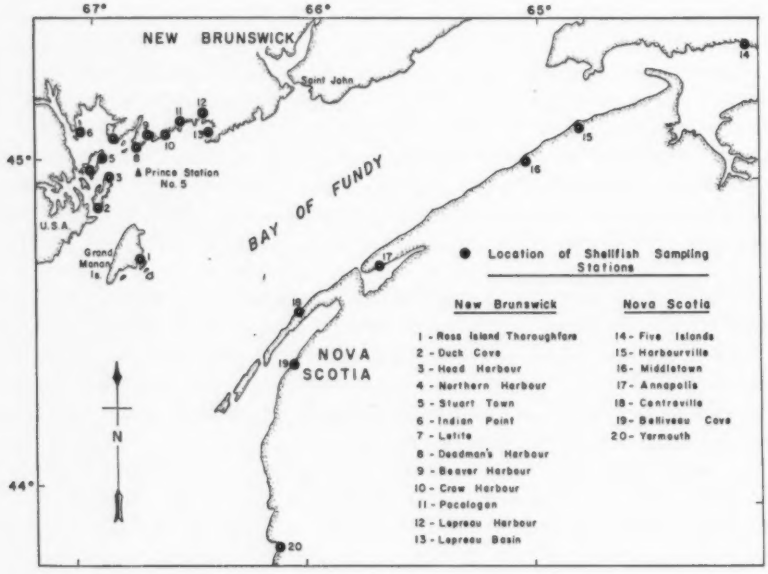

FIG. 1. Bay of Fundy showing location of shellfish sampling stations.

Of the 13 sampling stations on the New Brunswick side of the Bay of Fundy, 5 stations, Head Harbour, Lepreau Basin, Crow Harbour, Beaver Harbour and Ross Island Thoroughfare (Fig. 1) registered toxicity scores over 3000 micrograms (μg), much above the 1959 and 1960 averages. The other 8 stations also had significantly higher scores.

At Head Harbour, the principal monitoring station for the Bay of Fundy, the toxicity of blue mussels (*Mytilus edulis*) rose significantly during the second week of July and a peak score of 6080 μg was noticed on July 24. There was a sharp decline after the third week of September (Fig. 2; Table I). Most of the other stations showed a similar pattern.

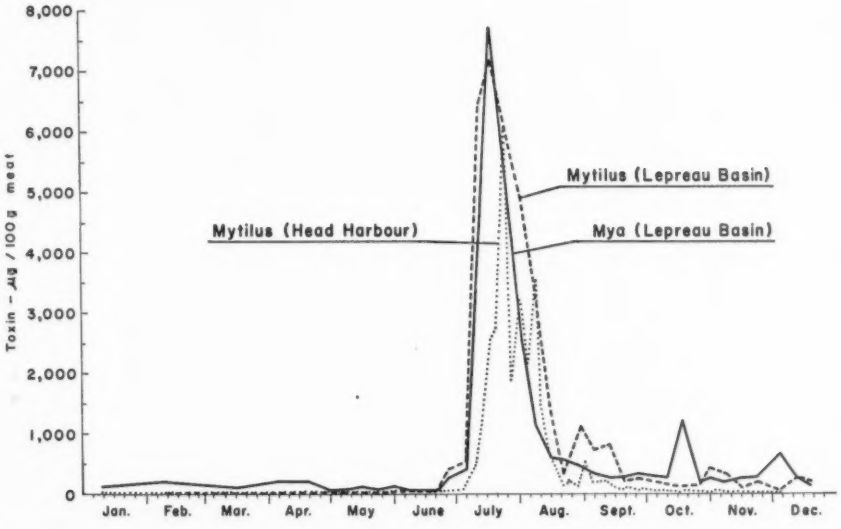

FIG. 2. Seasonal variations in shellfish toxicity levels in key areas in New Brunswick, 1961.

Another monitoring station, Lepreau Basin, on the other hand, showed some peculiar features. High scores were retained throughout the year in this area, particularly by soft-shell clams (*Mya arenaria*); whereas, blue mussels became toxic only after May. Peak scores for both mussels and clams ranged from 7200 to 7700 μg and were detected on July 18. A second lesser peak was observed in both clams (1184 μg) and mussels (432 μg) in October. As in most other years, the toxicity pattern at Head Harbour and Lepreau Basin began with a sudden increase in July and a gradual decline after August (Fig. 2).

On the Nova Scotia side of the Bay of Fundy, scores were significantly lower than those recorded on the New Brunswick side, but much higher than those recorded for Nova Scotia in 1959 and 1960. Only 5 of the 7 sampling stations showed any toxicity and the highest score of 960 μg was recorded at Centreville on July 25.

TABLE I. Shellfish toxicity scores from typical affected areas as related to the abundance of *G. tamarensis* in 1961 (+ = occasional; ++ = common; +++ = very numerous).

Month	Half-month period	Mean toxicity (μg/100 g) Head Harbour (*Mytilus*)	Lepreau Basin (*Mytilus*)	Lepreau Basin (*Mya*)	Abundance of *Gonyaulax*
Jan.	1st	...	< 32	96	...
	2nd	...	...	...	...
Feb.	1st	< 32	< 32	176	...
	2nd	...	...	...	...
Mar.	1st	...	< 32	62	...
	2nd	< 32	...	...	...
Apr.	1st	32	32	208	...
	2nd	...	< 32	192	...
May	1st	40	33	60	...
	2nd	56	33	97	...
June	1st	36	38	69	+
	2nd	...	217	164	++
July	1st	451	3472	2600	+++
	2nd	3280	7200	7700	++++*
Aug.	1st	1944	4240	1792	+
	2nd	299	939	544	...
Sept.	1st	168	760	296	+
	2nd	68	220	268	...
Oct.	1st	45	131	280	...
	2nd	34	233	549	...
Nov.	1st	33	344	200	...
	2nd	...	135	272	...
Dec.	1st	< 32	181	496	...
	2nd	...	192	138	...

*Peak abundance on July 31, 1961.

The problem of variability in sampling toxic shellfish is one that needs special consideration. Shellfish taken from different beds of the same inlet showed variations in poison content, but within limited sections of the beach such as those involved in our regular samplings at Head Harbour and Lepreau Basin, these differences were not large enough to warrant serious considerations. Individual variations in toxicity levels were noticed within and between species of shellfish. As a rule, mussels had a higher poison content than soft-shell clams; bar clams, on the other hand, accumulated five to ten times as much poison as soft-shell clams and mussels throughout the summer months.

PLANKTON STUDIES

RECONNAISSANCE

Regular plankton collections have been made twice each month since January 1961 at Head Harbour, N.B., and studied for species composition. As a standard procedure, the collections have been made by horizontal tows of 15 minutes' duration using ½-metre conical plankton nets in the upper 2 metres of water. Preliminary trials using No. 18, 20, and 25 bolting silk nets indicated that any net coarser than No. 25 is unsuitable to collect *Gonyaulax* efficiently. Both fresh and formalin-preserved samples were examined for dinoflagellates.

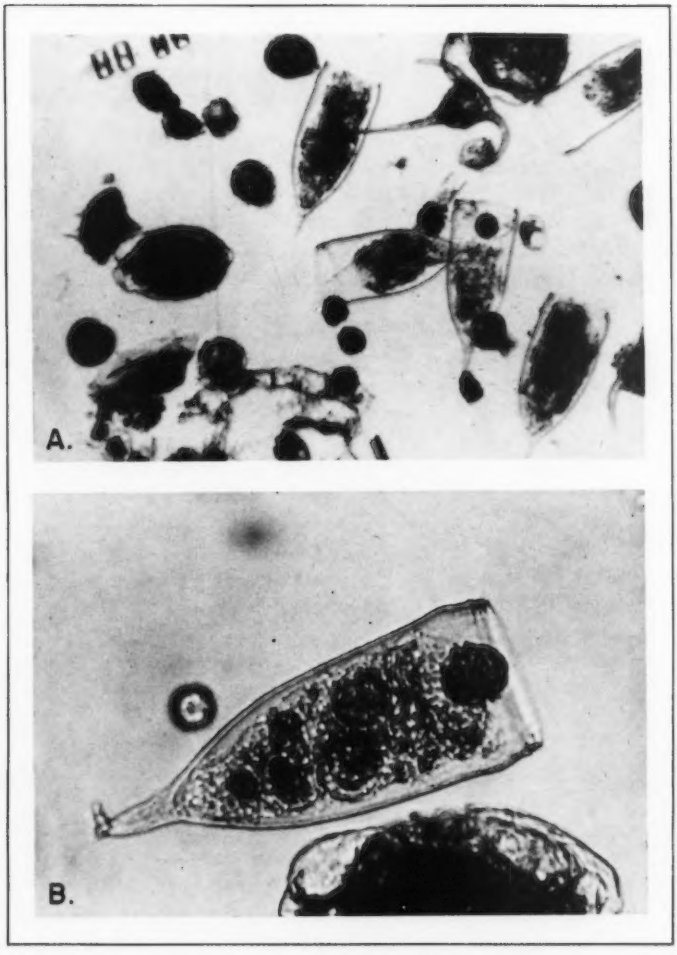

FIG. 3. Predation of *G. tamarensis* by *Favella* sp. **A.** General composition of the plankton collected at Head Harbour during peak toxicity season. Note abundance of dinoflagellates and *Favella*. ×100. **B.** Single *Favella* shown under higher magnification, at least six *G. tamarensis* can be seen in a semi-digested state within its body. ×250.

First appearance of *G. tamarensis* as an "occasional" plankter was noticed in the second week of June. Its subsequent abundance in late July coincided with the rise in shellfish toxicity at Head Harbour and Lepreau Basin (Table I). As a rule, the abundance of *G. tamarensis* in plankton either accompanied or preceded all increases in the shellfish toxicity. No such relationship could be established for other species of dinoflagellates. During the peak toxicity, surface water temperature at "Prince" Station No. 5 was about 10° C and salinity was around 31.3‰.

No *G. tamarensis* were noticed in Head Harbour plankton after September. Large ciliates of the genus *Favella* were noticed in the plankton during July and August but were very abundant in September (Table II). On several occasions a fairly large number of dinoflagellates, including *Gonyaulax tamarensis*, were found intact or in semi-digested state within the bodies of these ciliates (Fig. 3).

TABLE II. Seasonal abundance of the various dinoflagellates and *Favella* in plankton collected at Head Harbour, N.B., in 1961 (+ = occasional; ++ = common; +++ = very numerous).

	Dinoflagellates					
Month	*Ceratium*	*Peridinium*	*Exuviaella*	*Dinophysis*	*Gonyaulax*	*Favella*
Jan.	+++	...	...	+	...	...
Feb.	(No Observations)					
Mar.	+	...	...	+	...	...
Apr.	...	...	...	+	...	...
May	+	+	...	+	...	...
June	...	++	...	...	+	+
July	++	++	...	+	+++	++
Aug.	+	+++	+	...	+	++
Sept.	+	+	+	+	++	+++
Oct.	++	+	+	...	...	+
Nov.	++	+	...	...	...	+
Dec.	+	+	...	...	...	+

Judging from the extent of predation in our samples it appears likely that *Favella* and other allied genera of ciliates are responsible for selective feeding and subsequent disappearance of *G. tamarensis* from plankton. Needler (1949) observed a similar phenomenon and identified *Favella ehrenbergii* as the principal enemy of *G. tamarensis*. In our collections at Head Harbour, we were unable to find any ciliate recognizable as *F. ehrenbergii*. The most commonly occurring form in the Bay of Fundy collections was very similar to *F. panamensis* described by Kofoid and Campbell (1929). Other predatory ciliates of lesser importance were identified as *F. serrata* and *Parafavella denticulata*.

TOXIN IN PLANKTON

The apparent relationship between the abundance of *G. tamarensis* in plankton and the rise in shellfish toxicity prompted attempts to extract the toxic principle from plankton. The main object of these experimental observa-

tions was to ascertain whether or not it was possible to demonstrate measurable amounts of poison in plankton at the time when incidence of *G. tamarensis* in inshore waters was high. A simple but crude method of extraction, suitable for use while at sea, was adopted to obtain plankton extracts.

PREPARATION OF PLANKTON EXTRACT. Fresh live plankton was collected using a No. 25 bolting silk net (15 minute horizontal surface tow) and the contents were stored in a precooled thermos flask. Within a few hours the plankton was concentrated by centrifugation and then poured into a graduated cylinder. The concentrate was resuspended in an equal volume of 0.18*N* hydrochloric acid and boiled for 5 minutes. After cooling, the liquid was transferred again to a graduated cylinder and its original volume was restored by the addition of distilled water. pH was adjusted to between 2.5 and 3.5 using 0.1*N* sodium or ammonium hydroxide. The clear extract was recovered by recentrifugation.

Extracts were sent to the Laboratory of Hygiene, Department of National Health and Welfare, Ottawa, for bioassay. The results obtained are reported in micrograms of toxin per 100 ml plankton extract.

Plankton extracts were prepared from May to September and bioassay results are shown in Table III. Toxin was first detected in Head Harbour

TABLE III. Demonstration of paralytic toxin in plankton extracts.

Date	Locality	Toxin (μg/100 ml extract)
May 30, 1961	Head Harbour	< 32
June 13, 1961	Head Harbour	< 32
June 26, 1961	Lepreau Basin	< 32
June 29, 1961	Head Harbour	< 32
July 14, 1961	Head Harbour	32
July 24, 1961	Head Harbour	154
July 31, 1961	Head Harbour	2560
Aug. 10, 1961	Lepreau Basin	53
Aug. 14, 1961	Head Harbour	< 32
Aug. 21, 1961	Head Harbour	< 32
Sept. 7, 1961	Head Harbour	< 32
Sept. 18, 1961	Head Harbour	< 32

plankton on July 14 and a score of 32 μg/100 ml was reported. On July 31 there was a sudden rise to 2560 μg (16,000 mouse units). During this period of high toxicity the incidence of *G. tamarensis* in the plankton was also very high (Table I). No poison was detected in Head Harbour plankton during August and September.

GONYAULAX TAMARENSIS OF THE BAY OF FUNDY

UNIALGAL CULTURES

The coincidence of peak abundance of *G. tamarensis* and peak levels of toxicity of shellfish and plankton was indicative but not convincing evidence that this dinoflagellate was the primary source of poison in shellfish. Efforts were

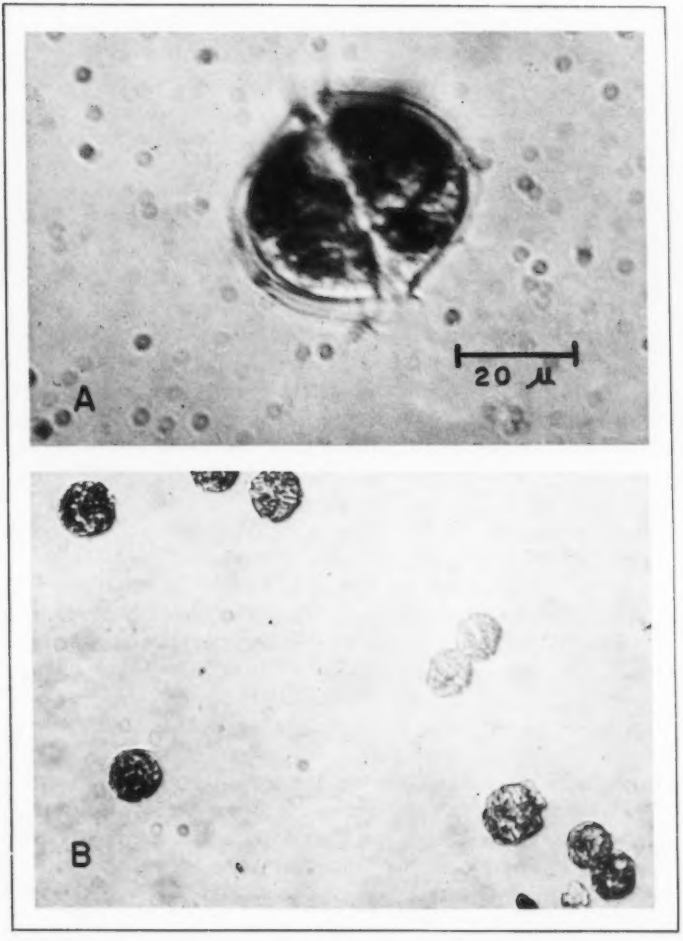

FIG. 4. *Gonyaulax tamarensis* of the Bay of Fundy. **A.** Typical cell form from a unialgal culture showing an equatorial girdle and smooth enclosing theca. ×1000. **B.** Dividing cells or "duplets" during early growth phase of the culture. ×250.

therefore directed towards growing *G. tamarensis* from the Bay of Fundy in unialgal cultures so as to permit a simple test of the toxicity of this species of dinoflagellate.

There was another important reason for trying to obtain unialgal and, if possible, axenic cultures of *G. tamarensis*. We wished to study its growth requirements, the effect of various physical and chemical factors on its growth, and certain characteristics of the toxin it appeared to produce. It was hoped that laboratory studies co-ordinated with field observations would provide a better understanding of what causes dinoflagellate blooms in the Bay of Fundy and elsewhere where shellfish become toxic. Such knowledge would be useful in predicting when and where shellfish might be expected to become toxic and in determining the feasibility of control measures.

Isolation of *G. tamarensis* from live plankton was accomplished in July 1961 when the incidence of this species at Head Harbour was very high. Cells for unialgal cultures were isolated by micro-pipetting (Pringsheim, 1946), followed by repeated washings with millipore-filtered sea water (ultra filter). The cells were finally transferred into 20- × 125-mm culture tubes containing 10 ml of a selected medium. Temperatures were maintained at 8–12° C during pipetting and washing and cultures were grown in a temperature-controlled room at 10 ± 1° C under constant illumination (400–500 ft-c) provided by banks of 40-watt cool fluorescent lamps.

Of 9 enriched marine media tested, Erd-SCHREIBER and ASP 7 (Pintner and Provasoli, 1958) supported best growth and were used for growing mass cultures. Population densities as high as 2500 cells per ml were obtained within 4 weeks after an initial inoculum of 1–3 cells per ml. Every care was taken to ensure that cultures were bacteria-free. Specimens for inoculations were serially washed during successive transfers and autoclaved media were used. There is no doubt that by these procedures bacterial contamination was kept to a minimum but we make no claim that the cultures were axenic.

These cultures have been maintained since July 1961 by serial transfers in Erd-SCHREIBER and ASP 7.

Population growth in culture is exponential and is accomplished by asexual fissions. Growth was measured by counting cells at regular intervals with an inverted plankton microscope (Utermöhl, 1936). Short chains or "duplets" with two individuals are quite common during the early growth phase (Fig. 4B) but chains with 3 to 4 individuals, which are quite common in *G. catenella* of the Pacific coast, are rarely seen. Individual cells are yellowish-brown or yellowish-green in colour and swim freely in a characteristic spiral motion. Live cells are spherical, with smooth outer thecae which are shed upon coming in contact with strong chemicals like acid and formalin or when the cells are exposed to abrupt temperature changes. Well marked equatorial girdles can be seen in both live and preserved specimens (Fig. 4A). Cell dimensions vary from 30 to 40 microns.

TAXONOMIC STATUS

During the early phases of our culture work, much helpful information on growth characteristics and growth requirements of *G. tamarensis* was obtained

from working with unialgal cultures of the type form of this species. This was originally isolated from the Tamar River estuary, near Plymouth, England. These cultures were grown in our laboratory from stock cultures kindly supplied by Dr L. Provasoli of the Haskins Laboratories, New York. Apparently the same dinoflagellate from the Bay of Fundy which is now suspect has been identified as *G. tamarensis* by several workers (Needler, 1949; Gran and Braarud, 1935) and we have accepted their identifications. After isolating and raising it in mass cultures it was possible to compare the English and Canadian forms. Mass cultures of both were maintained under identical conditions of light, nutrients and temperature.

Bioassay of acid extracts made from unialgal cultures revealed that the English form was non-toxic and the Canadian highly toxic. This led to speculation that (1) our form might be a different species, or (2) possibly a different strain of the same species as is found in the Tamar River estuary, England, or (3) the English form might have lost its toxicity during the many successive generations in culture in the laboratory. The possibility of the last explanation is remote since our cultures of Fundy *Gonyaulax* grown for several generations for more than a year have remained as toxic as the parent stock. Furthermore, as far as we are aware, the association of *Gonyaulax tamarensis* with shellfish poisonings in England has never been definitely established. A comparative morphological study of typical specimens of the two forms was therefore undertaken in collaboration with Mr Adam Bursa of the Fisheries Research Board of Canada, Arctic Unit, to establish the taxonomic status of the Fundy form. This study is still in progress; nevertheless, our preliminary observations suggest that the Bay of Fundy *Gonyaulax tamarensis* does not show sufficient morphological differences to warrant its separation as a species distinct from the English form described by Lebour (1925). In cultures, however, we did observe that the incidence of morphological aberrants was always higher in the Bay of Fundy form than in the Plymouth form, although both were grown under identical conditions. Our present attitude is to regard this difference and the difference in toxicity between the English and Canadian forms as indicative of the existence of different strains of the same species. Further work is needed in this field.

TOXIN FROM *GONYAULAX TAMARENSIS* CULTURES

The development of unialgal cultures of the Bay of Fundy *G. tamarensis* paved the way to a better understanding of the role of this species in the paralytic shellfish poisonings. Shellfish are known to feed on plankton including marine dinoflagellates which may or may not be poisonous. Where poison is involved the shellfish may store it in different organs; for example, the digestive gland, gill or siphon, depending on the species of shellfish (Sommer and Meyer, 1937; Medcof *et al.*, 1947; Chambers *et al.*, 1952). An abundant supply of *G. tamarensis* in mass cultures made it possible to test the unialgal cultures for poison production both directly, by extracting toxin from the cells as already described for plankton, and indirectly, by feeding shellfish on mass cultures and subsequently testing them for poison.

Preparation of Culture Extracts

Paralytic shellfish poison has been shown to be water soluble, acid stable and moderately stable at high temperatures (Sommer *et al.*, 1948). For this reason extraction of the toxic principle from unialgal cultures was done by acid hydrolysis using 1.0*N* hydrochloric acid. pH was maintained between 2.5 and 3.5. Two procedures were followed. In the first, a specified volume of culture was treated *in situ* with hydrochloric acid. In the second procedure, cells were harvested from a known volume of culture by microfiltration (Millipore HA filter) or by high-speed centrifugation prior to treating with hydrochloric acid. In both cases the extracts were prepared by boiling for 5 minutes and recentrifugation as was done previously for plankton extracts. These extracts were sent to the Laboratory of Hygiene, Ottawa, where they were subjected to the same type of bioassay as is used for extracts of shellfish.

Bioassay Procedure

The method currently in use for the detection and measurement of paralytic shellfish toxin involves the death response of mice. Extract (1.0 ml) is injected intraperitoneally into each of three test mice weighing between 19 and 21 grams. If all three mice survive, the results are reported as negative (< 32 μg or <200 mouse units[2]). If any of the mice die, the extract is diluted so as to give death time between 4.5 and 7 minutes in response to a 1.0-ml injection.

Ten mice are then similarly injected and the median death time is calculated. From the median death time, mouse-unit values are determined using Sommer's Time-Toxicity Table. All mouse units are rounded off to two significant figures. The number of mouse units per ml of acid extract is obtained by multiplying the number of mouse units by the dilution factor and from this number mouse-unit values/100 ml are calculated.

Mouse units are converted to micrograms of poison by multiplying the number of mouse units by a conversion factor or CF value which is determined by the strain of mice used as test animals. The CF value determined for the strain used in the Laboratory of Hygiene, Ottawa, for shellfish toxin bioassay is 0.16.

Bioassays of culture extracts have scored as high as 123 μg/100 ml of original culture. Extracts made from cell concentrates always gave higher scores than *in situ* culture extracts (Table IV). This discrepancy appears to be partly due to the presence of sodium ions in the culture medium which reduces the sensitivity of the mouse test (Schantz *et al.*, 1958; Wiberg and Stephenson, 1960).

SHELLFISH FEEDING EXPERIMENTS

The purpose of these experiments was to provide additional evidence of the toxic nature of *G. tamarensis* and also to measure the rate of toxin uptake by the shellfish when fed on mass cultures. Non-toxic and toxic soft-shell clams (*Mya*

[2]A mouse unit is defined as the amount of toxin in 1 ml of an extract which when injected intraperitoneally will kill a 20 g mouse in 15 minutes with symptoms of paralysis and respiratory failure.

TABLE IV. Toxicity of *Gonyaulax tamarensis* cultures, with particular reference to *in situ* and cell concentrate extraction.

Tube no.	Cell density/ml		Days after inoculation	Toxin (μg/100 ml culture)	
	Initial	Final		*In situ*	Filtered cells
1	10	9×10^3	61	53	54
2	10	8.4×10^3	68	50	51
3	10	1.3×10^4	73	53	72
4	10	1.2×10^4	82	66	70
5	10	1.6×10^4	89	70	78
6	10	1.8×10^4	96	70	78

arenaria) were fed on unialgal cultures of *G. tamarensis* of the Bay of Fundy over a certain time period and their toxicity estimated at intervals by bioassay.

FEEDING OF NON-TOXIC CLAMS

About 400 clams were procured from a toxin-free area near St. Andrews, N.B. After thorough washing with sea water, the clams were subjected to a conditioning period of 1 week in an aquarium containing millipore-filtered and aerated sea water maintained at 10° C. At the end of this period almost all of the clams had gotten rid of accumulated debris and food particles as determined by examination of gills and digestive gland. About 200 of these clams were then transferred to a glass feeding tank with approximately 5 l of unialgal culture of the Bay of Fundy *G. tamarensis* (population density approximately 1.9×10^4 cells/ml). The remaining lot was kept as a control in millipore-filtered sea water. Both control and experimental lots were kept in a temperature-controlled room at 10° C under constant illumination.

Daily samples of 25 clams were removed from both experimental and control lots and extracted for bioassay. Density of the dinoflagellates in the feeding tank was measured by daily counts of cells per millilitre. Poison was first detected in clams on the second day after they were placed in the feeding tanks, and by the sixth day toxicity had risen to 112 μg. There was a progressive decline in the cell density indicating active feeding by clams on *G. tamarensis* (Fig. 5). The controls which were not fed on culture remained non-toxic and scored < 32 μg throughout the experiment.

FEEDING TOXIC CLAMS

About 100 clams were procured from Lepreau Basin, N.B. — a station where high toxicity scores are retained throughout the year. The experimental stock was divided into four lots of 25 clams each and kept in four separate glass tanks with filtered sea water. After a week of conditioning as in the previous experiment, three lots received different amounts of *G. tamarensis* culture while the control lot remained unfed. After about 8 days the feeding clams were removed from their respective tanks and extracted for bioassay. There was no trace of *G. tamarensis* in the tanks on the eighth day when the shellfish were removed

indicating that the clams had removed the dinoflagellates. The results obtained in this experiment (Table V) provide additional evidence of the relationship between the number of dinoflagellates consumed and the rise in shellfish toxicity.

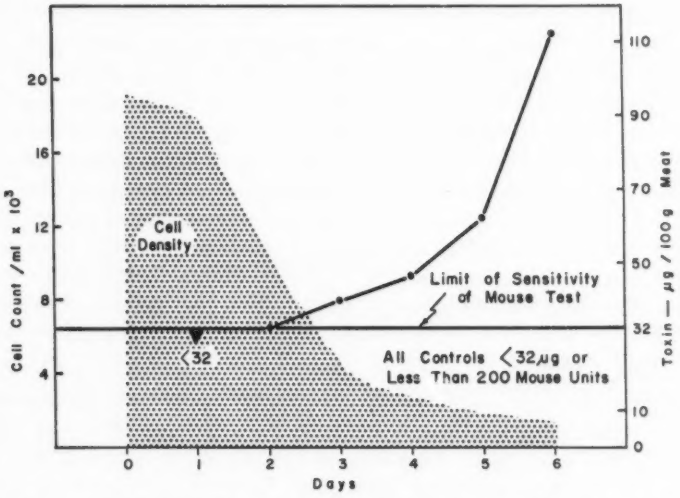

FIG. 5. Accumulation of toxin in clams as a result of consumption of *G. tamarensis* during a 6-day feeding test.

TABLE V. Accumulation of toxin by soft-shell clams from Lepreau Basin as a function of number of *Gonyaulax tamarensis* consumed.

Group (25 clams)	Vol. of culture fed (ml)	Estimated number of cells eaten	Toxin level (µg)
A (Control)	0	0	176
B	1200	2.28×10^7	200
C	1400	2.66×10^7	192
D	2000	3.80×10^7	240

DISCUSSION AND CONCLUSIONS

The results of this study show quite conclusively that the real source of shellfish poison in the Bay of Fundy is *Gonyaulax tamarensis*. The possibility that bacteria present in unialgal cultures of *G. tamarensis* may be the source of toxin can be ruled out since bacteria-free cultures have also yielded high scores (Provasoli, personal communication). In their study of paralytic shellfish poison on the Pacific coast, Sommer *et al.* (1937) implicated *Gonyaulax catenella* as the primary source of poison. Commenting on the variability in toxin pro-

duction by *G. catenella*, Sommer (1939) pointed out that 1 mouse unit was obtained from 3000 to 200,000 organisms. From the higher toxicity scores yielded by relatively few cells in our cultures and plankton samples, we are inclined to believe that the Bay of Fundy *G. tamarensis* has a higher toxin content per cell than *G. catenella*. Experiments are in progress to substantiate this supposition.

G. tamarensis appears to be of wide occurrence in the North Atlantic. On the North American side, besides the Bay of Fundy, this species has been found in the Gulf of Maine (Gran and Braarud, 1935) and the Canadian eastern arctic (Bursa, 1961). On a recent plankton survey of the estuary of the St. Lawrence, the writer found an abundance of *G. tamarensis* near Metis Beach and Capucins on the south shore which coincided with high shellfish toxicity scores in these areas. This species has also been found in plankton samples collected in the Gulf of St. Lawrence along the Gaspé peninsula. *G. tamarensis* has been reported as far south as Puerto Rico (Burkholder *et al.*, 1960; Margalef, 1961) but no case of paralytic shellfish poisoning has come to light from that region. From evidence in hand, we are inclined to believe that the southernmost range of toxic shellfish is the coast of Maine.

On the eastern side of the North Atlantic, *G. tamarensis* has been reported in coastal waters of Great Britain (Lebour, 1925), Norway (Braarud, 1945) and Portugal (Silva, in press). This species has also been found in the *Michael Sars* North Atlantic Expedition collections (Gaarder, 1954). A recent report of shellfish poisonings in Scotland links *G. tamarensis* to the outbreak (Gemmill and Manderson, 1960).

While implicating *G. tamarensis* as the primary causative organism in the Bay of Fundy, the author is not ruling out the possibility of other species of dinoflagellates as being toxic. It is quite likely that the additional "kicks" in toxicity scores during fall and winter months might be due to such dinoflagellate populations which follow summer dominance of *G. tamarensis* in the general event of phytoplankton succession. Unlike the west coast, we have not encountered discolouration or "red water" phenomenon in the Bay of Fundy even during the maximum abundance of *G. tamarensis* and at no time did we find "blooms" of this species in the accepted sense of the word.

The laboratory studies in co-ordination with field observations have provided sufficient basic information on cause and effect relationship between shellfish toxicity and dinoflagellate abundance. This is one important step closer to our main objective, viz., setting up a basis of reliable prediction of danger periods from year to year, but much more remains to be done. We are extending our observations on growth and toxigenic characteristics of *G. tamarensis* in unialgal cultures in the laboratory. At the same time we are intensifying and refining our sampling program in order to examine critically the ecological relationships between the toxic shellfish and dinoflagellates on one hand and between the various environmental factors and dinoflagellates on the other. From this we hope to deduce what factors or combination of factors regulate the seasonal abundance of *G. tamarensis* in nature and hence of levels of toxicity in shellfish.

ACKNOWLEDGMENTS

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Accelerated Cooling of Wet, Heavily Salted Fish[1]

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ABSTRACT

"Green" heavily salted split fish may be pre-cooled within a cold storage area with ice and salt, without imposing an excessive load upon storage refrigeration facilities and with little additional labour. Twelve pounds of ice plus 4 lb of salt per 100 lb of fish, uniformly applied between 3- to 4-inch thick layers of fish, will reduce the bulk fish temperature by 25 F° (14 C°) in less than 8 hours.

No mechanical equipment is required if flake ice be deemed a commodity. The direct cost may be estimated at less than 15 cents per 100 lb of finished (dried) fish.

Pre-cooling is not essential under normal conditions but is recommended for heavily salted fish in which the degree of red bacterial contamination is unknown or suspected to be critical, and the storage refrigeration is not adequate to cool the product in a sufficiently short time.

INTRODUCTION

The purpose of this investigation is to find an economical method for pre-cooling green, heavily-salted, split fish.

Such fish is usually brought to be drying plant during the summer and fall and is held in cold storage at 35 to 40° F (1 to 4° C). This temperature is judged to be suitable for the inhibition of the growth of red bacteria (Castell, 1950), the appearance of which on salted fish downgrades the quality. Most of the existing storages are designed to maintain this temperature even under summer conditions, but have little additional refrigeration capacity to cool large quantities of warm fish, which they may be called upon to accept during a relatively short period of time.

To make the most efficient use of storage space, there is a tendency to pile fish as high as the ceiling height will allow. Warm fish stored in this manner may require several weeks to reach the safe, storage temperature. The rate of heat dissipation from the fish may be increased by making smaller, shallow piles, with air spaces between. This introduces additional labour for re-piling and requires much larger floor areas than are normally available.

When exceptionally large shipments are received, the refrigeration capacity may not be adequate to cool the product quickly enough, regardless of the distribution of fish within the storage space. Moreover, when fish of unknown origin is received (or red bacteria activity is suspected) it must be brought to a safe temperature as quickly as possible. These considerations serve to illustrate the need for a method by which fish may be pre-cooled independently of the storage facilities.

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Many attempts have been made to design suitable pre-cooling equipment for this product. As early as 1939, a continuous-type apparatus was designed by engineers of the Fisheries Research Board of Canada. This, like subsequent designs, could not be justified because of the increased capital expenditure to provide for the additional refrigeration equipment and building space to house it. Further, the operation added appreciably to the labour cost of admitting fish to storage.

Previous investigations in this field have favoured either the refrigerated air blast or the brine spray or dip. Upon checking the first mentioned, it was found that "green", split heavily-salted cod, between 2 and 3 lb weight, in −12° F (−24° C) air blast of 800 ft/min, were cooled from 65 to 35° F (18 to 1° C) in about 10 minutes.

A pre-cooler using this principle, capable of handling 10,000 lb of fish per hour, would require a moving belt at least 4 ft wide and 100 ft long if loaded at 2½ lb/sq ft. Obviously, such a machine, with its attendant refrigeration equipment, may discourage any but the largest operators.

Dips and sprays present similar pictures of awkward, space-demanding, costly installations, adding capital and operational costs which this industry can ill afford.

Two industrial salt fish producers were consulted. Both agreed that some method of pre-cooling could be most useful. The industry's lack of acceptance of air blast, dip or spray seemed to confirm the above evaluation.

EXPERIMENTS AND RESULTS

For many years fresh fish has been cooled by storage in ice. Provided that sufficient salt was added to prevent the ice-water from freshening the salt fish, might not such a method be feasible for pre-cooling this product?

To verify this hypothesis, 800 lb of green salt fish were piled in the usual manner, but with a layer of ice and salt added to every third layer of fish (3–4 inches thick). The experiment was carried out at room temperature 68.5° F (20° C) which would be expected to have little effect on the rate of cooling near the middle of the pile, because of the low rate of heat transfer through bulk fish encountered in industrial storages.

Twenty pounds of ice plus 6 lb of salt were used for 100 lb of fish, the thickness of the ice-salt layer varying from zero at the edges to a maximum at the centre of the layer. This, in effect, doubled the rate of application of ice plus salt per 100 lb of fish in the middle region of the pile. As shown in Fig. 1, the temperature of the fish in the middle of the pile was reduced from 65 to 35° F (18 to 1° C) in 50 minutes or less, and continued to fall to nearly 0° F (−18° C). Fish temperature around the edges of the pile varied from room temperature to as low as 32° F (0° C), presumably because of drainage of brine from the pile.

Obviously this cooling rate was unnecessarily rapid and the final temperature attained was needlessly low. Further consultation with the industry indicated that little could be gained by reducing the fish temperature below 35° F (1° C)

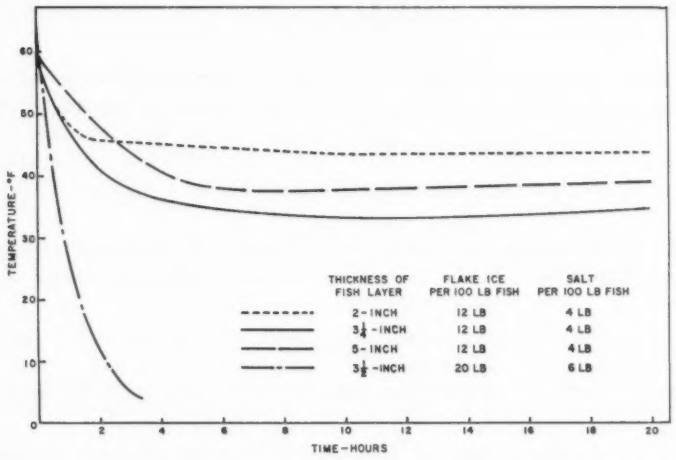

FIG. 1. Temperature changes in "green", heavily salted, split cod while being cooled with ice and salt, in pile.

but that this temperature should be reached within 8 hours after admission to storage.

Accordingly, further experiments were undertaken in a commercial salt fish storage. The controlled temperature, herein, is normally 35° F (1° C) but the actual temperature while admitting fish (doors open) is extremely variable. The experiments were carried out at a room temperature of 58° F (14° C), this being definitely higher than could be anticipated under operating conditions.

A ratio of 12 lb flake ice and 4 lb salt per 100 lb of fish was calculated to be adequate to bring the fish to 35° F (1° C) under the test conditions, without the use of ice and salt becoming excessive.

Of the various combinations investigated, three thicknesses of the fish layer, 2, 3¼ and 5 inches were judged to be significant. Description of the construction of the 5-inch layer pile is as follows, and is typical of other layer thicknesses:

On a pallet, raised about 4 inches above the floor, the first layer of fish, weighing about 600 lb, was laid to cover an area 79 inches long by 39 inches wide. A thermocouple was inserted near the center of the thickest portion of a fish and this fish was placed in the middle of the layer. Seventy-two pounds of flake ice and 24 lb of salt were then spread on top of this layer of fish, slightly more heavily toward the center than at the edges. A second layer of 600 lb of fish was then added with a second thermocouple placed in a manner similar to the first one. A second layer of ice and salt was then added. This procedure was repeated until the fifth and final layer of ice and salt.

The relative cooling rates for layer thicknesses of 2, 3¼ and 5 inches using 12 lb of ice and 4 lb of salt per 100 lb fish are shown in Fig. 1, together with the rate for the 3½-inch layer when using 20 lb of ice and 6 lb of salt.

CONCLUSIONS

It would appear that 12 lb of ice plus 4 lb of salt is sufficient to pre-cool 100 lb of fish as admitted to a refrigerated storage capable of maintaining 35° F (1° C). The thickness of the fish layer, between icings, is not too critical within the limits of 3 to 5 inches. Under normal storage conditions of 35° F (1° C), the fish temperature should be reduced from 60 to about 35° F (15 to 1° C) in 8 hours or less.

Analysis of the fish so treated showed only slightly lower salt content. When finally dried, iced fish were judged to be of a quality equivalent to uniced fish.

The direct cost has been estimated at about 10 cents per 100 lb green or 15 cents per 100 lb finished dried fish. This assumes flake ice to be a commodity which may be purchased at $6.50 per ton, salt at $20 per ton and labour at $1.25 per hour.

It is not suggested that all fish received will require such a treatment. Much high quality salt fish has been and is being produced without pre-cooling. This procedure is suggested as a possible practical method for use where storage refrigeration is not adequate to take care of a high product load, when plant intake is abnormally large or where the degree of red bacterial contamination is suspected to be critical.

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Zwicker and Company Limited, Lunenburg, N.S. contributed the use of their plant, their product and the services of their personnel.

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Life History of Redside Shiners, *Richardsonius balteatus*, with Particular Reference to Movements In and Out of Sixteenmile Lake Streams[1]

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ABSTRACT

Movements of shiners through two-way traps on inlet and outlet streams of a small British Columbia lake were studied from 1956 to 1962. The date on which adults first entered the inlet each spring corresponded to the first rise of daily maximum stream temperature above 10°C. Days on which increased numbers of shiners ascended the inlet were positively associated with days of rising daily maximum water temperature, and were not associated with water levels. Egg deposition occurred both in daylight and darkness. Downstream movement of shiner fry was greatest during periods of turbidity, and occurred largely during darkness. Shiners first spawned at age III or older; some lived to age V or VI. Number of adult shiners over 79 mm fork length was estimated by Petersen marking experiments to be about 13,000 in the 42-acre lake. A large interchange of adults took place in some years between the lake and parts of the watershed upstream; a small interchange occurred downstream. Many shiners entered a stream more than once each year. Many survived to spawn in two or more successive years. Movement into the streams varied markedly in different years and was small compared with the number of adults in the lake. Homing is suggested as a mechanism which determines the proportion of inlet-, outlet-, and lake-spawning in this species.

INTRODUCTION

The redside shiner, *Richardsonius balteatus* (Richardson), is a small cyprinid native to the Pacific slope of North America, where it is abundant and widespread. It has received attention from some biologists because of its spectacular but puzzling morphological variation, and from others because of its well-documented impact on sport fisheries for rainbow trout. It has so far defied most attempts of the former to rear it, and of the latter to eradicate it.

The present study is based largely on trapping and marking conducted from 1956 to 1962 on streams entering and leaving a small lake in central British Columbia. The number of shiners marked over a 2-year period was roughly one-third the standing population of adult shiners in the lake. These data have yielded previously unrecorded information on the life history of the species, including something of its vital statistics, spawning migrations, population interchange between lakes, and lakeward movement of the fry.

The program was supported by the Fish and Game Branch, Department of Recreation and Conservation, as part of a study on life histories of species important to sport fisheries.

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LITERATURE ON THE SPECIES

In 1953, Lindsey reviewed literature on the redside shiner to that date, including its nomenclature, structural variation and distribution. Life history of the species has recently been discussed by the following authors: Weisel and Newman (1951); Lindsey (1953); Weisel (1957); Carl, Clemens and Lindsey (1959); Crossman (1959a), who presents information on the horizontal, vertical, diurnal and seasonal movements of shiners in Paul Lake; and Johannes and Larkin (1961) who discuss feeding behaviour.

Anal fin ray count is said to be positively correlated with developmental temperature in British Columbia (Lindsey, 1953) but negatively correlated with temperature in Montana (Weisel, 1955a). This paradox is still unresolved, although there is general agreement regarding a tendency to develop more anal fin rays towards the north in this species (Lindsey, 1956; Weisel, 1961). Slight but significant differences in ray count occurred between successive year-classes of shiners reared in a spring of constant water temperature (Weisel, 1961).

The effect of introduction of redside shiners on rainbow trout in the Paul Lake system in British Columbia has been studied intensively (Larkin and Smith, 1954; Crossman, 1959a, b; Crossman and Larkin, 1959; Johannes and Larkin, 1961).

Hybrids have been reported between redside shiners and peamouth club (*Mylocheilus caurinus*), northern squawfish (*Ptychocheilus oregonensis*), and longnose dace (*Rhinichthys cataractae*), both in British Columbia (Carl *et al.*, 1959) and in Montana (Weisel, 1954, 1955b). Earlier Schultz and Schaefer (1936) described hybrids between redside shiners and speckled dace ("*Apocope oscula carringtoni*") in Washington and Oregon.

DESCRIPTION OF THE STUDY

Sixteenmile Lake (also called Baker Lake) lies at an elevation of about 2700 feet (823 m), 10 miles (16 km) northeast of Quesnel in central British Columbia. The lake (Fig. 1) has a surface area of 42 acres (0.2 km^2), a maximum depth of 24 feet (7.3 m), and a mean depth of 12 feet (3.6 m). It has rather low dissolved solids (60 parts per million), early and well-defined thermocline formation, and severe summer oxygen depletion below 12 feet (3.6 m). Both the lake and creek water are brown-stained, with Secchi disc readings of about 3 to 4 feet (1–1.2 m). The shores are floating marginal mats, the bottom is ooze-covered, and there is little exposed gravel except on the small delta of the inlet creek. The lake lies in the Central Interior climatic region where annual precipitation ranges between 20 and 30 inches (51–76 cm), with heaviest rain in June.

In addition to redside shiners, Sixteenmile Lake contains populations of rainbow trout (*Salmo gairdnerii*), white suckers (*Catostomus commersonii*), longnose suckers (*C. catostomus*), and northern squawfish (*Ptychocheilus oregonensis*). There is no resident population of Dolly Varden (*Salvelinus malma*), but during three years' study 3 juveniles of this species were captured entering Sixteenmile Lake from its outlet.

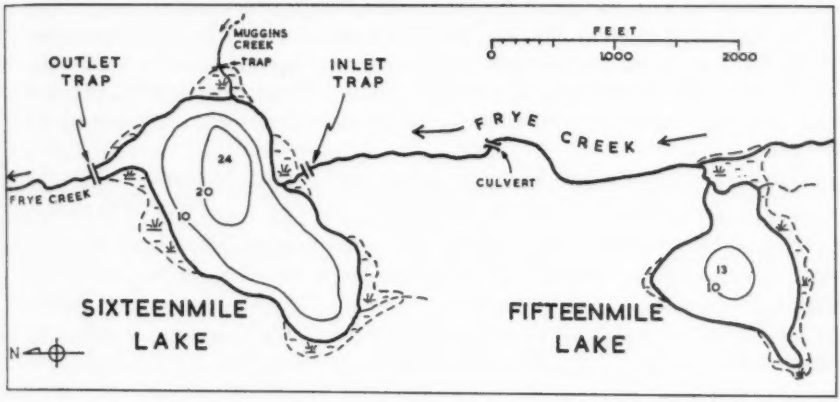

FIG. 1. Map of Sixteenmile Lake and adjacent watershed, showing location of two-way fish traps. Depth contours of lakes in feet (1 foot = 305 mm).

The inlet trap, a two-way trap situated within 100 yards (91 m) of the lake, consisted of a diagonal screen fence with leads and holding boxes at each end, modified from the design of Shetter (1938). During most periods of operation the fence and boxes were fitted with $\frac{3}{4}$-inch (19-mm) square mesh galvanized wire screen; at some periods of low stream flow screen of $\frac{1}{8}$-inch (3-mm) square mesh was substituted.

The short stretch of creek bottom between the inlet trap and Sixteenmile Lake is an unstable mixture of gravel and silt patches. Upstream of this trap, Frye Creek occupies a wooded ravine, with alternate swift gravel-bottomed riffles and deeper slow-flowing silt-bottomed stretches often with undercut banks. Depths vary from 2 inches to 3 feet (5–91 cm), and widths from 2 to 10 feet (61–305 cm). Between Sixteenmile Lake and the tributary from Fifteenmile Lake, Frye Creek passes through a culvert under the Barkerville Road; this is passable in both directions to fish, except at very low or high discharge when ascent is blocked.

Fifteenmile Lake is smaller than Sixteenmile (Fig. 1) but similar in character, with stained water and a floating marginal mat. It has no permanent tributary, and drains to Frye Creek through a small swamp. The 5 species of fish listed for Sixteenmile also have been taken in Fifteenmile Lake. Two other lakes and some ponds are tributary to upper Frye Creek; the largest of these (Kenny Lake) yielded no fish when gillnetted on July 4, 1957.

Sixteenmile Lake drains via a tapering arm blocked by an old beaver dam, leading to the lower part of Frye Creek (Fig. 1). Prior to construction of the outlet trap this dam formed a block to ascent of fish except during periods of high water. The outlet trap, set into the dam, was a modified Wolf-type trap (Wolf, 1951) designed to capture fish moving either upstream or downstream. Leads and panels were of $\frac{1}{8}$-inch (3-mm) square mesh wire screen.

Below Sixteenmile Lake, Frye Creek is largely gravel-bottomed. Two other lakes comparable to Sixteenmile are tributary to it; of these at least one, Davie Lake, supports populations of rainbow trout and longnose suckers. Frye Creek enters the Cottonwood River about 3 miles (5 km) downstream of Sixteenmile Lake and about 18 miles (29 km) above the entry of the Cottonwood into the Fraser River.

Traps were operated from early May to late August in 1956, from early May to late June in 1957, and from April or early May until late May or June in 1958, 1960, 1961 and 1962. Traps were usually attended at least once and often twice each day. All fish were examined and passed through in the direction they had been moving when captured. In some years most shiners were marked by fin clips which indicated the site and direction of first capture. A notch was cut in either the upper or lower edge of either the dorsal or ventral lobe of the caudal fin, or in a combination of two such places. These marks were clearly recognizable even when the fin had completely regenerated one or more years later. Figure 2 shows a regenerated clip in the lower edge of the dorsal caudal lobe. The sex and presence or absence of clips were recorded for every shiner handled. Periodically samples of shiners were measured (fork length).

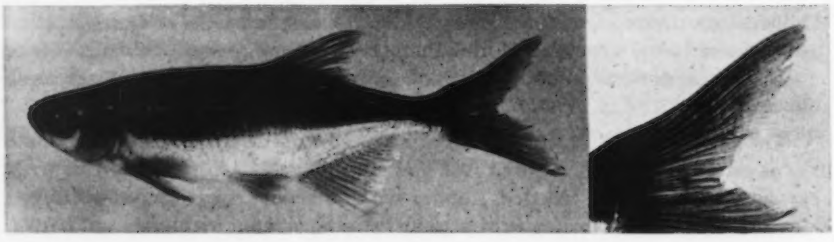

FIG. 2. Adult redside shiner (fork length 109 mm) recaptured in 1957, with regenerated 1956 caudal fin clip (enlarged at right).

Stream temperatures were measured with continuous temperature recorders and maximum-minimum weather thermometers. Stream levels were recorded from vertical graduated rules. Outlet stream temperatures and levels, not given here, are shown for 3 years by Northcote (1962; fig. 30).

Muggins Creek (Fig. 1) is a small intermittent tributary entering the east shore of Sixteenmile Lake. On May 18, 1957 a two-way trap of $\frac{3}{4}$-inch (19 mm) square galvanized screening was installed in Muggins Creek about 150 yards (137 m) upstream from its mouth. The trap was operated until June 22 when low creek level prevented entrance of fish. During this period only 4 shiners had moved upstream as far as the trap, although over 200 longnose sucker spawners, 3 white sucker spawners, over 60 squawfish and several immature rainbow trout had passed through. In 1958 the trap was operated from April 19 to May 27, during which time a number of juvenile rainbow trout ascenders, but no redside

shiners, were taken. During periodic survey of the creek in May 1959, 1960, 1961 and 1962 longnose sucker spawners were occasionally noted but no redside shiners were seen. Apparently very few shiners spawn in this inlet creek although other cyprinids and catostomids do so. Water temperature of Muggins Creek averaged 3–5° C lower than Frye Creek throughout the period of study. Although Muggins Creek was always cooler than Frye Creek, its maximum daily temperature frequently rose above 10° C, at which temperature shiners readily enter Frye Creek.

IDENTIFICATION OF SHINER FRY

Shiner fry moving downstream were sampled with Surber stream samplers suspended in the current. Sucker fry were easily distinguished from cyprinid fry by their larger size (12–19 mm total length in late June) and forward position of the anus (preanal 69–74% of total length). The two cyprinid species, redside shiners and squawfish, were often taken together, and were more difficult to separate.

The following diagnostic features (some visible in Fig. 3) apply to shiner fry from 7.5 to 8.5 mm, and to squawfish fry 8.5 to 9.6 mm total length. Most migrant fry fell in these size ranges, although a few smaller individuals with yolk sacs still visible were also captured moving downstream. These had probably been displaced forcibly from the gravel by spawning suckers and squawfish.

The anus is farther forward in shiner than in squawfish fry, with preanal lengths (snout to posterior margin of anus) usually less than 63.0% of total length in the former and more in the latter; 90% of migrant cyprinid fry were distinguishable on this basis alone.

Shiner fry have a mass of large melanophores around the dorsal surface of the swim bladder. These form a black line apparently continuous in lateral view (Fig. 3) with a strip of large melanophores, mostly in contact with each other, running along the ventral edges of the myotomes back to the caudal peduncle. On the dorsal surface a double row of large melanophores extends from the back of the head to the peduncle. Many of these and the lateral melanophores are almost as big as the pupil of the eye, in contrast to squawfish of comparable size, whose melanophores are usually much smaller than the pupil. Shiners also have a median pigment mass ventral to the pericardium directly between the pectoral bases; squawfish have not.

In squawfish fry the melanophores around the swim bladder are more diffuse and paler than in shiners (greyish rather than blackish), and the ventrolateral and dorsal rows are less striking and are composed of much smaller spots. Slightly larger squawfish fry show on each side a concentration of melanophores overlying the ventral tip of the hypural plate; this becomes the distinctive black caudal spot that is present in all juvenile squawfish and is lacking in shiners.

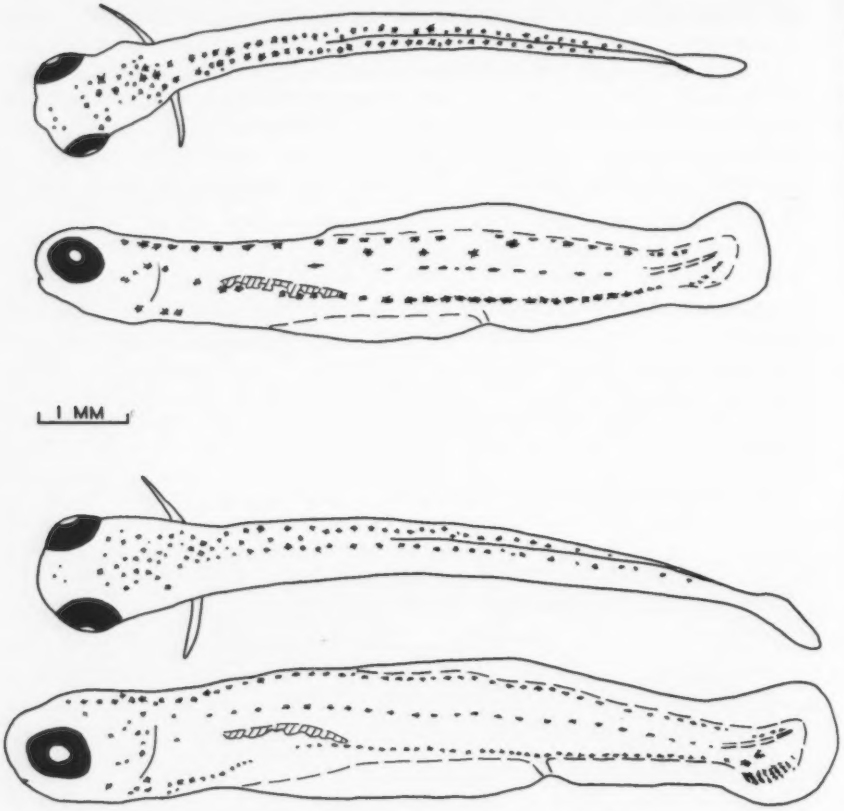

FIG. 3. Dorsal and lateral views of fry of redside shiner *Richardsonius balteatus* (top pair), and northern squawfish *Ptychocheilus oregonensis* (bottom pair). Traced from a photographic enlargement. Hatched area indicates internal pigmentation dorsal to swim bladder.

SEASONAL TIMING OF ENTRANCE TO INLET

Mature shiners entered Frye Creek sporadically throughout late spring and summer in 1956 (Fig. 4); few were recorded after mid July although traps were operated until August 21. At water levels below −10 cm, entry of fish into the inlet trap was seriously restricted, probably contributing to the decline in shiners ascending the inlet after mid July in 1956 and mid June in 1957 (Fig. 4).

The date on which shiners first began to enter Frye Creek varied considerably from year to year (May 19 in 1956, April 26 in 1961). Timing of first entrance into the spawning stream (based on 6 years' observations) was not related to stream level but rather to stream temperature. A close association existed between the date on which the maximum stream temperature first rose above 10° C and the date on which the annual accumulated run first exceeded 5 fish

(Fig. 5). Shiners began to enter the stream each year about the time daily maximum stream temperatures rose above 10°.

Males were predominant in early phases of the spawning run while females were more abundant towards the end of the run. Marked day-to-day fluctuations occurred in numbers of mature shiners ascending Frye Creek. These changes were particularly evident in 1956 (Fig. 4), but also occurred in all other

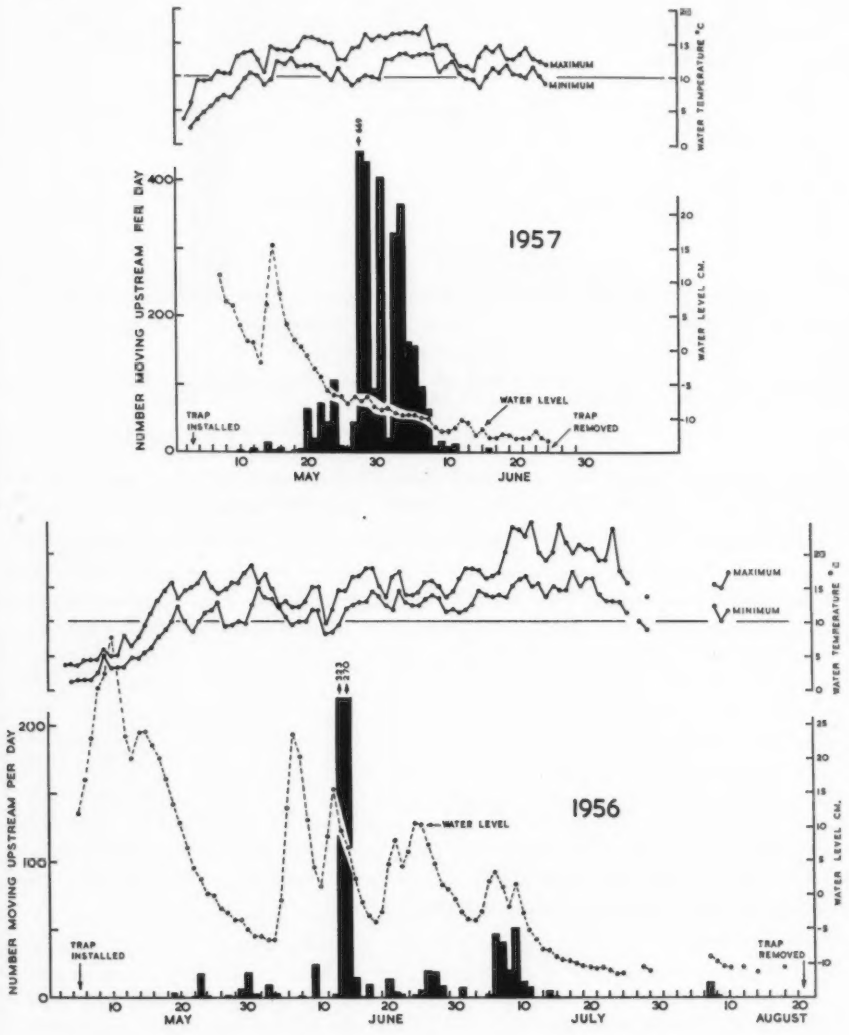

FIG. 4. Seasonal timing of ascent of adult shiners through inlet trap in two years.

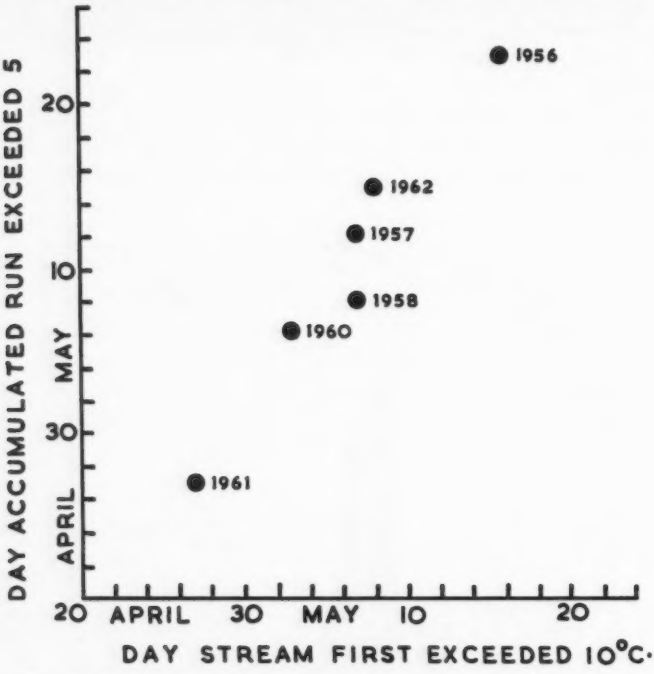

FIG. 5. Date of first warming of inlet stream above 10°C, plotted against date when over 5 adults had ascended stream.

years studied. Of 28 marked increases in daily number of shiners ascending the creek (1956–1961), 23 were associated with days on which the maximum water temperature was higher than that of the previous day. This relation between daily changes in shiners moving upstream and changes in water temperature was examined by regression analysis using logarithmic transformation. Numbers of shiners moving upstream on one day were expressed as a fraction of those moving upstream on the previous day. All counts of ascending shiners were increased by 10 to reduce effect of small changes on days when few fish moved upstream. Six Celsius degrees were added to all changes in daily maximum water temperature to avoid negative numbers. Data for 117 days (1956–1961) were treated. Increases in numbers of shiners ascending Frye Creek were positively associated ($P < 0.05$) with rises in daily maximum stream temperature, although there was considerable variability (correlation coefficient $r = 0.194$). No association with water level was evident.

DIEL[3] TIMING OF ENTRANCE TO INLET

Numbers of shiners entering the inlet trap were counted at approximately 2-hour intervals for a 42-hour period, June 6–8, 1957 (Fig. 6). Most shiners

[3]*Diel* refers to the 24-hour period of a day and a night.

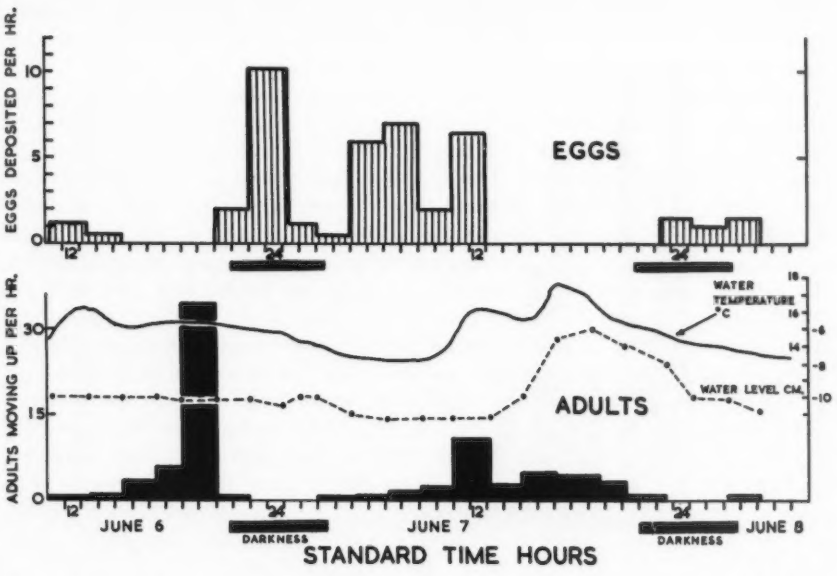

FIG. 6. Diel timing of egg deposition on sample stones (top), and of ascent of adult shiners through inlet trap (bottom), on June 6–8, 1957.

(both males and females) moved upstream during the afternoon and evening. Virtually none entered the trap during darkness. Timing of movement had no obvious association with changes in water temperature or level during this period.

MOVEMENT INTO OUTLET STREAM

Movement of mature shiners into the outlet stream of Sixteenmile Lake was recorded at the outlet trap from April 21 to August 15, 1956 and from May 5 to June 25, 1957. In 1956, 61 unmarked and 3 marked mature shiners (29 males and 32 females) moved into the outlet between May 10 and July 19; none was taken before or after this period. Twenty-five shiners descended into the outlet trap during its operation in 1957. Apparently a few mature shiners enter the outlet stream sporadically during the summer; never more than 5 fish were taken on any one day.

EGG DEPOSITION

In 1957, groups of shiners displaying apparent spawning activity were first seen in the inlet creek on May 28, some 18 days after the first shiner had entered the stream. Activity similar to that described by Weisel and Newman (1951) was observed in a riffle at a depth of about 4 inches (10 cm) approximately 10 to 15 feet (3–4.6 m) downstream from the inlet trap. Fresh shiner eggs, taken in a Surber sampler placed immediately below the site of activity, indicated that

spawning was probably taking place at that time (mid afternoon). A number of recently fertilized shiner eggs were found adhering to stones in another riffle near the inlet trap and at the first riffle above the lake.

On the evening of June 5, 1957, 10 stones approximately 2 inches (5 cm) in diameter were each marked with a small yellow latex spot and placed in the riffle immediately below the inlet trap. Between June 6 and 8 each stone was examined for shiner eggs every 2 hours. Any eggs found were removed and the stones replaced in the riffle. Periods of active egg deposition (Fig. 6) occurred during both the day and night and bore no obvious relation to upstream movement of adult shiners or to water temperature and level. No significant difference ($P > 0.10$) was noted in number of eggs deposited in daylight and darkness during a 6-day period (June 6–12). Examination of the standard stones was continued until June 25, 1957, but no fish eggs were found after June 21. In 1956 spawning below the inlet trap was observed at least as late as July 20.

In summary, egg deposition in the inlet stream occurred from late May to late June in 1957, but probably for a longer period in some years when entrance of adults was earlier (e.g. early May in 1960) or when high stream flow persisted for longer (e.g. at least until late July in 1956). Egg deposition by redside shiners, observed previously to be nocturnal in some localities (Lindsey, 1953) and diurnal in others (Weisel and Newman, 1951), occurred both in daylight and darkness.

DOWNSTREAM MOVEMENT OF FRY

Seasonal Timing

Recently emerged shiner fry moving down Frye Creek were captured in a standard one-foot-square Surber sampler fitted with fine nylon netting of about 0.7 mm diameter mesh. The sampler, anchored firmly onto the stream bottom a short distance upstream from the inlet trap, strained approximately one-quarter of the stream discharge throughout most of the study period. The sampler was checked at least once a day, and usually both morning and evening. Fry and debris collected were preserved in 10% formalin solution for later examination. Methods of identifying shiner fry have been described previously.

In 1957, shiner fry moving down Frye Creek first were taken on June 7, ten days after the sampler was installed in the stream. Few fry were captured until mid June (Fig. 7). The sampler was not operated after June 26.

Between the probable date of first spawning (May 28) and first capture of fry moving downstream, 10 days later, average daily water temperature rose gradually from about 12° to 15°, with daily maxima as high as 16° C (Fig. 4). Previous experiments produced hatching of shiner eggs in 11 days at 15° (Lindsey, 1953). According to these data, the first fry to move down Frye Creek evidently had not spent an appreciable time in the gravel following hatching, and were probably displaced downstream very soon after emergence. On the other hand, Weisel and Newman (1951) describe newly hatched larvae as much smaller (5.3 mm) and less well developed than those taken moving downstream in Frye Creek. Their fry, however, had developed in an aquarium at higher temperature and may also have hatched prematurely due to artificial agitation.

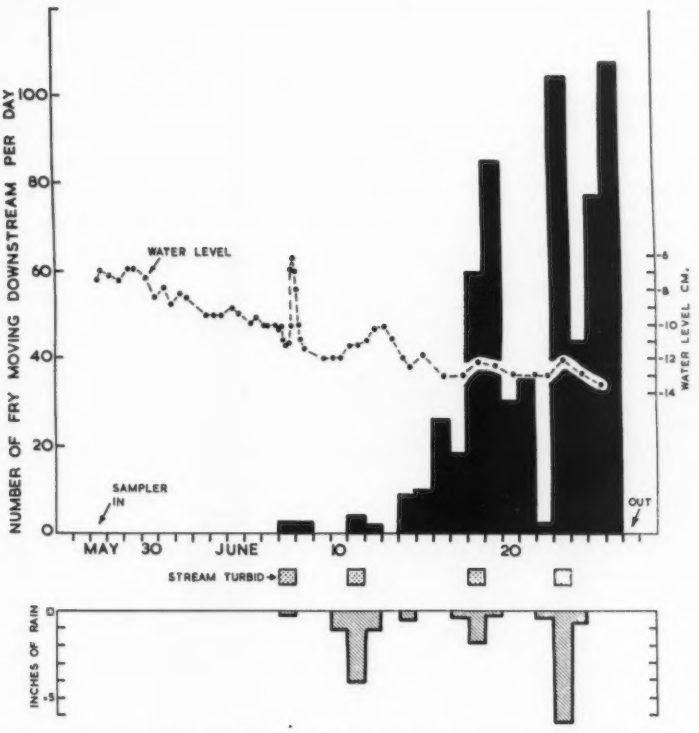

FIG. 7. Seasonal timing of Surber sampler catches of downstream-moving shiner fry, Sixteenmile Lake inlet, 1957.

Marked daily changes occurred in numbers of shiner fry moving down Frye Creek (Fig. 7). Several of the sudden increases in downstream movement were associated with rises in creek level and muddy water brought about by heavy thunder showers. Particularly striking was the decline in fry moving downstream between June 21 and 22, during a period of stable creek level and little rain, followed by the sudden increase in downstream movement on the night of June 23 when heavy rain raised the creek and made it very turbid (Fig. 7).

DIEL TIMING

Between June 21 and 23, 1961 a Surber sampler was installed a short distance downstream of the inlet trap and emptied every 2 hours during the day and every hour at night. Approximately 75% of the creek discharge flowed through the sampler.

Most fry moving downstream did so in darkness (Fig. 8). Differences in timing and numbers of fry moving downstream on the two successive nights may be related to differences in nocturnal illumination as shown for rainbow trout

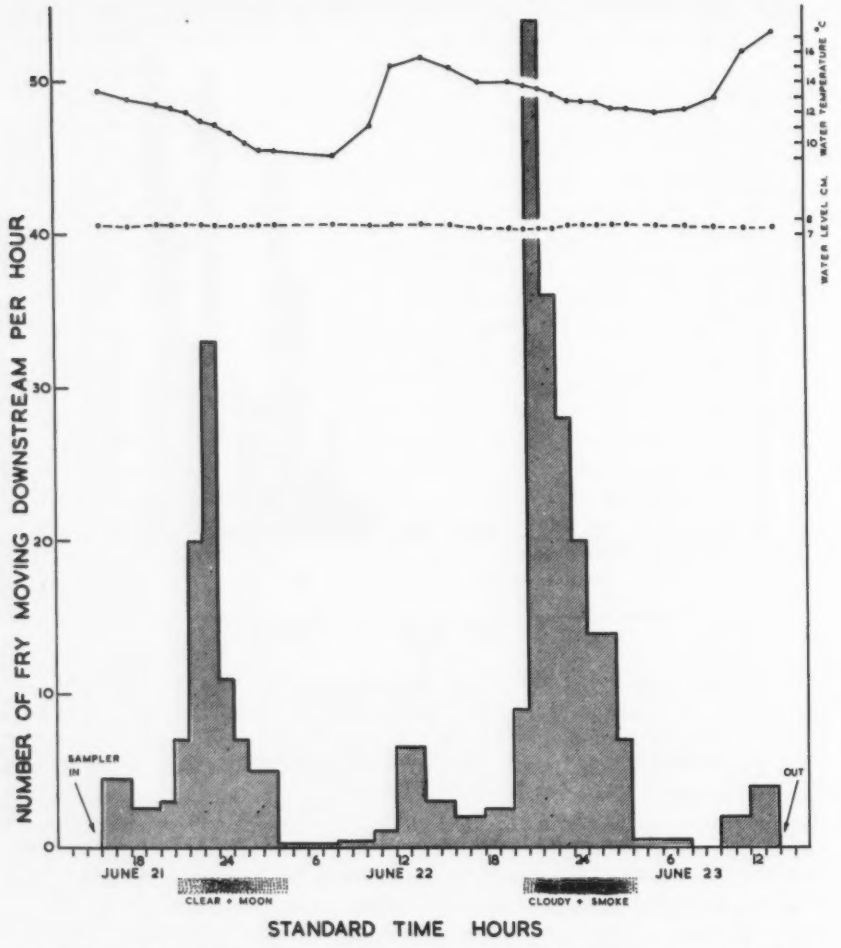

FIG. 8. Diel timing of Surber sampler catches of downstream-moving shiner fry, June 21–23, 1961.

fry by Northcote (1962). Between 2100 and 0400 hours on June 21–22, a total of 88 fry moved downstream into the sampler, while 173 did so during the same period the following night. On the night of lesser downstream movement there was moonlight with no cloud cover; on the next evening a 50–90% cloud cover combined with smoke from forest fires resulted in a much darker night. Nearly twice as many fry moved downstream that night.

A few fry also moved downstream in the afternoon of each day studied (Fig. 8). These fry may have been displaced by the spawning activities of white suckers during the afternoon rise in water temperature.

AGE AND GROWTH

The frequency distribution (bottom of Fig. 9) shows sizes of fish in combined samples taken by seining and gillnetting in Sixteenmile Lake in June 1956 and June 1957. Sex was determined, by examination of the gonads, only in fish over 70 mm long (fork length). Some but not all of the larger individuals taken in the lake contained ripe eggs or enlarged and active testes. A bar is included indicating newly emerged fry captured while entering the lake from the inlet creek at a mean length of 8 mm.

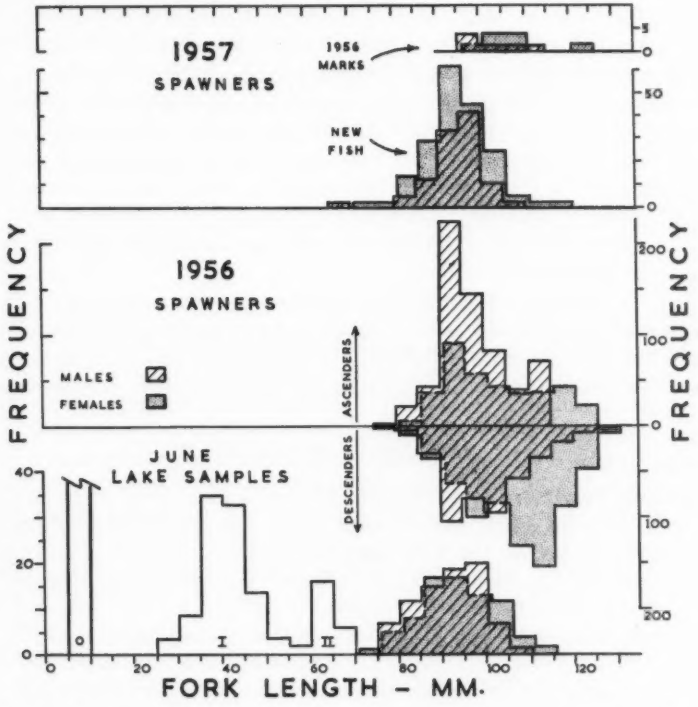

FIG. 9. Length–frequency distributions of shiners in Sixteenmile Lake. Both marked and new descenders are included amongst 1956 spawners. See text for source of samples.

Also shown in Fig. 9 are size–frequency diagrams for the 1956 and 1957 spawning runs to the inlet creek. The histogram for 1956 represents size–frequency of the entire run (adjusted for incomplete sampling as described later), while the 1957 histograms are based only on samples taken on May 29 and June 6–8.

Year-classes 0, I and II are marked opposite 3 size–frequency peaks on the bottom of Fig. 9. Most spawners are evidently age III or older. Beyond the modal size of 90 mm, age cannot be determined reliably from size–frequency,

but a second peak amongst 1956 spawners at 110 mm suggests that many of these may be age IV or older. These age interpretations are substantiated by aging of redside shiners in several other British Columbia localities using size–frequency distributions of larger samples.

Growth is evidently slow amongst adult fish in Sixteenmile Lake. All shiners handled in the 1956 inlet spawning run were marked by fin clipping, and many of these were recaptured spawning again in 1957. Lengths of a sample of 17 of these recaptures are shown at the top of Fig. 9. Although larger than most of the unmarked fish taken in the same sample (shown immediately below), these recaptures do not lie at the extreme upper size limit of the 1956 spawners. These marked fish were known to be spawning at least a second time, and the largest female may well have been spawning a third time.

The view that Sixteenmile Lake shiners spawn in several successive years is supported by the recapture, on May 29, 1959, of 5 clipped fish amongst a sample of 145 inlet spawners. These fin clips (regenerated but clearly distinguishable as in Fig. 2) had been applied in the 1956 or 1957 spawning runs, so their owners when recaptured were apparently spawning either a third or fourth time. If they had first spawned at age III (fourth summer of life) then they were in their sixth or seventh summer.

There is a greater proportion of females amongst the larger size groups in all histograms in Fig. 9, as well as in other gillnet and seined samples from Sixteenmile and Fifteenmile Lakes. Populations from other British Columbia lakes show the same tendency towards a disproportion of females amongst the larger fish.

POPULATION ESTIMATES

The total number of adult shiners (80 mm or longer) in Sixteenmile Lake may be estimated from the number of fish which were marked in the 1956 spawning run and recovered in the 1957 spawning run. In Table I inlet and outlet marks are grouped together. "Marks at large" excludes marked fish known to

TABLE I. Population estimate of shiners over 79 mm fork length at time of marking, based on recovery in 1957 spawning run of 1956 marks.

Sample size (includes only fish over 89 mm)	2311
Recaptures	185
Marks at large	1058
Population estimate	13,151
95% confidence limits (Ricker, 1958)	10,589–17,598

be above the inlet trap or below the outlet trap at the time of sampling. Fish which were marked ascending the inlet in 1956 but which were not subsequently retaken were assumed not to have returned to Sixteenmile Lake during periods when the trap was inoperative. The assumptions are made that there was no differential mortality between marked and unmarked fish, and that there was no habitual failure to migrate among shiners of the size used.

An attempt has been made to allow for one year's growth between marking and recovery by excluding from the 1957 samples all fish under 90 mm. This crude correction is based on the fact that almost no fish marked in the 1956 spawning run were under 80 mm (Fig. 9), and it seems unlikely from the growth rates between ages 0, I and II that any fish over 80 mm in 1956 would have been under 90 mm in 1957. This correction is probably conservative (i.e. the minimum size to be included in the 1957 sample should probably be somewhat above 90 mm) and is therefore an improvement over population estimates in which no allowance is made for growth.

The population estimate in Table I is based solely on fish marked in, and sampled in, the inlet spawning run. If spawning occurs elsewhere (e.g. in the lake), and if shiners which once spawned in the inlet tend to return there in subsequent years, then the estimate represents only the inlet-spawning segment of a larger total population in Sixteenmile Lake. Moreover, some fish may exceed 79 mm before first spawning, and some may not spawn each year; in either case the present estimate is too low. Because of these possibilities, coupled with the difficulty in correcting for growth, the estimate is at best only an approximation and is more likely to be low than high.

TOTAL ANNUAL MOVEMENT THROUGH TRAPS

In the first year of operation every shiner captured in either the inlet or outlet trap was marked distinctively, by fin clipping, according to its site of capture and the direction of movement. Many were recaptured one or more times the same year. A similar program was followed the second year, complicated by the fact that two easily distinguishable "year-classes" of marks were now involved. Consequently, by the end of 1957 a complex body of data was available concerning the numbers, size, sex ratio and histories of over 30 different categories of fish.

Total numbers of fish in these different categories are presented diagrammatically in Fig. 10. Each category indicated by a separate total is unique with respect to its site and direction of first capture and its known subsequent history.

For example (starting at the bottom of Fig. 10) 797 shiners were first captured moving downstream through the inlet trap in 1956. (These fish had probably originated from Fifteenmile Lake that year, as is explained later.) Of these, 1 fish passed through Sixteenmile Lake and was recaptured passing down through the outlet trap the same year. Five others returned back upstream through the inlet trap; of these, 3 which evidently overwintered upstream of the trap (probably in Fifteenmile Lake) were retaken the following year (1957) passing downstream through the inlet trap. A further 60 of the 797 new inlet descenders marked in 1956 survived the winter in Sixteenmile Lake and were recaptured ascending the inlet in 1957; of these, 11 returned downstream to the lake, and of these 5 again ascended the inlet the same year. One 1956 inlet descender was recaptured descending the outlet in 1957. The various fates of 956 fish first taken in 1956 moving *upstream* through the *inlet* trap can similarly be followed, as can those of the 61 new descenders and 30 new ascenders taken in the *outlet* trap in 1956.

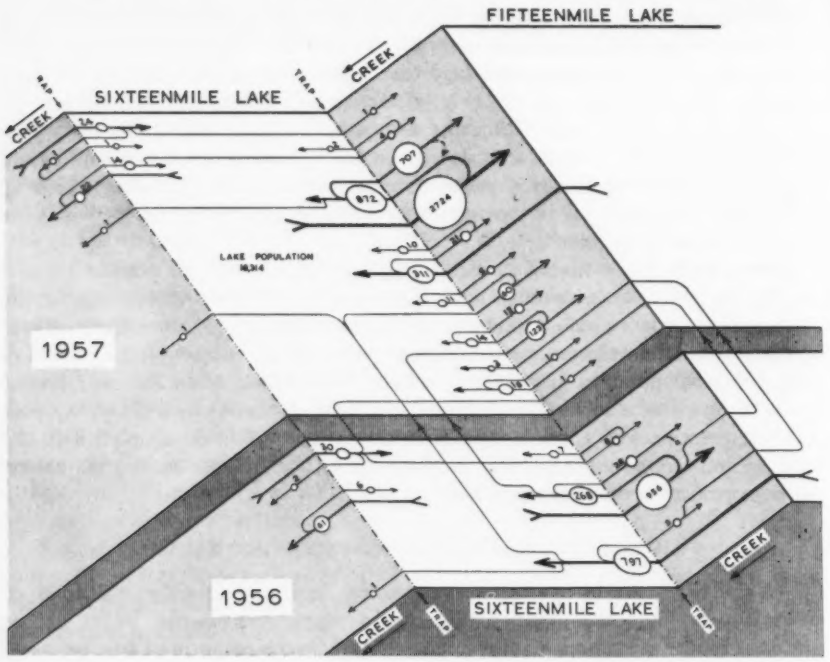

FIG. 10. Diagrammatic summarization of movement of marked shiners through the inlet and outlet traps of Sixteenmile Lake in 1956 (*bottom*) and 1957 (*top*). Figures (and area of accompanying circles) indicate numbers of each category of fish captured passing through traps in direction of arrow. Each category in each year is unique in its previous history and direction of movement when captured. A few individuals with complex or uncertain histories are omitted. See text for further explanation.

In 1957, in addition to the various types of 1956-marked recoveries, there are again 4 main categories of new fish (new ascenders and new descenders, in inlet and outlet) whose histories can be followed during that year.

Data on which Fig. 10 is based are shown (with the exception of outlet trap catches) in Table II, along with further information on sex and size distribution which will be referred to later. The following features of the net movement of adult shiners in and out of Sixteenmile Lake are apparent from Fig. 10 and Table II:

(*a*) A great deal more movement, both upstream and downstream, occurred through the inlet trap than through the outlet trap. The population interchange, and the amount of apparent egg deposition, was negligible at the outlet compared with the inlet. This was true not only for redside shiners but also for the squawfish and two species of suckers in Sixteenmile Lake.

(*b*) In each year, over two-thirds of the fish which started from Sixteenmile Lake that year and ascended the inlet did *not* return to the lake (at least until the end of trap operation, Fig. 4). Some of these probably moved on up to Fifteenmile Lake, as discussed later.

(*c*) Although all fish moving upstream through the inlet trap had been marked, a large proportion of those fish taken moving downstream were unmarked when first captured. These fish had presumably come from Fifteenmile Lake, as discussed later.

TABLE II. Numbers of shiners captured in Inlet Trap in 1956 and 1957, grouped according to "origin" (i.e. site, direction and year of *first* capture). Figures in parentheses show percentage of large fish (over 109 mm fork length).

Origin	Sex	Sequence of capture in Inlet Trap			
		1st ascent	1st descent	2nd ascent	2nd descent
1956 inlet ascenders					
1956 catches	♂	602(11)	157(22)	14(7)	...
	♀	354(28)	111(51)	14(14)	...
1957 catches					
Wintered above trap	♂	...	14	1	...
	♀	...	4	0	...
Wintered below trap	♂	...	...	88	9[a]
	♀	...	...	35	5[a]
1957 inlet ascenders					
1957 catches	♂	1516	462	568	...
	♀	1208	410	139	...
1956 outlet					
1956 catches	♂	4(0)	4(0)	...	...
	♀	4(0)	3(33)	...	...
1957 catches	♂	1	...	...	...
	♀	0	...	...	...
1957 outlet					
1957 catches	♂	4	2	...	...
	♀	1	2	...	...
		1st descent	1st ascent	2nd descent	2nd ascent
1956 inlet descenders					
1956 catches	♂	257(10)	2(0)	...	...
	♀	540(39)	3(0)	...	...
1957 catches					
Wintered below trap	♂	...	28	5	2
	♀	...	32	6	3
Wintered above trap	♂	...	...	3	...
	♀	...	...	0	...
1957 inlet descenders					
1957 catches	♂	175	17	7	...
	♀	136	4	3	...

[a]Of these, 9 males and 3 females subsequently reascended the inlet a third time.

(*d*) The failure of many inlet ascenders to return to Sixteenmile Lake (b) almost equalled the addition to the lake of new descenders (c) in 1956, and greatly exceeded it in 1957. The net gain through the inlet was 75 adults in 1956, the net loss was 2468 in 1957.

(*e*) The outlet trap also captured both new descenders and new ascenders in each year. The net exchange, negligible in contrast to the inlet (a), was a loss of 28 fish in 1956 and a gain of 14 fish in 1957.

(*f*) Many fish passed through the same trap three or more times in one year. (The marking system sometimes did not allow distinction between fish recaptured twice and those recaptured three or more times. For example, near the top of Fig. 10, the broken arrow indicates that the 872 fish descending through the inlet in 1957, all bearing a particular mark, probably included some which had already been recaptured as marked descenders and had been subsequently passed back upstream amongst the 707 ascenders.) This phenomenon, referred to as "re-entry" into the stream (in the same year) will be considered in more detail later.

(*g*) A tendency towards greater *upstream* movement in 1957 than in 1956 was evident in the following ways:

1. The net upstream loss in the inlet stream was greater in 1957 (d). In 1957 many more fish originating from Sixteenmile Lake ascended through the inlet trap than in 1956, and in 1956 many more fish originating from Fifteenmile Lake descended through the inlet trap than in 1957.

2. The net exchange through the outlet slightly favoured downstream movement in 1956 and upstream movement in 1957 (e).

3. Amongst fish originating in Sixteenmile Lake and first caught ascending through the inlet trap, a much larger proportion of those which returned downstream to the lake subsequently reascended the inlet a second time during the same year in 1957 than in 1956.

4. Migration into the inlet stream not only involved more fish in 1957 than 1956, but the main upstream surge occurred some two weeks earlier (as discussed previously).

In summary, much more movement of shiners occurs at the inlet than at the outlet. A large interchange of adults evidently can take place between Sixteenmile Lake and parts of the watershed farther upstream, and a small amount with areas downstream of the lake. Some interchange of adults occurs between inlet and outlet. Many fish re-enter a stream more than once in a year, and many survive to spawn in two or more successive years. The total number of fish involved in all these movements through the traps varies markedly from one year to another, and is small compared with the estimated population of adults in the lake.

IMMIGRATION INTO SIXTEENMILE FROM FIFTEENMILE LAKE

Many unmarked fish were trapped descending into Sixteenmile Lake from its inlet stream in 1956 and 1957. The size and sex distribution of these fish precludes the likelihood that they had somehow escaped capture while previously ascending from Sixteenmile Lake the same year, or that they were undetected

clip recoveries. It is also most unlikely that appreciable numbers of shiners had already entered the creek from Sixteenmile Lake before the trap was installed in the spring. The creek was screened for two weeks in 1956 before the first shiner was taken. Previous to trap installation the creek was solidly ice-covered, with very low flow and very few pools which could provide refuge to fish.

The most satisfactory conclusion seems to be that the unmarked fish descending Frye Creek into Sixteenmile Lake came downstream from Fifteenmile Lake (or possibly from other parts of the watershed above Sixteenmile Lake). Gillnet sets in Fifteenmile Lake caught all five fish species found in Sixteenmile Lake, and no barrier existed to downstream movement between the two lakes.

Of descenders taken in the inlet trap in 1956, unmarked fish (from Fifteenmile Lake) included a much higher percentage of females (68%) than did marked fish (41%) (Table II). A higher proportion of these females were small amongst the unmarked than the marked descenders (Table II), and their sexual condition was different. To quantify this, on June 6 and 7, 1957 all females captured in the trap were categorized as either "gravid" (i.e. still containing ripe or near-ripe eggs) or "spent" (i.e. thin flanks, evidently spawned-out). Of the 141 descending females which were known by their marks to have come from Sixteenmile Lake that year, only 21% were still gravid. In contrast, of the 37 descending females which were unmarked and had presumably moved down from Fifteenmile Lake, 54% were still gravid when passed through the trap. At that time 95% of females ascending from Sixteenmile Lake were classed as gravid.

The contribution of fish from Fifteenmile to Sixteenmile Lake is not therefore one solely of spent fish dropping downstream exhausted after the spawning act. The fact that over half the females in this group were not spent despite their downstream movement suggests that their exit from Fifteenmile Lake may have been accidental or in pursuit of food, rather than as a direct prelude to spawning. The outlet of Fifteenmile is a protected area with very little gradient; in contrast the outlet of Sixteenmile Lake, where no such exodus occurred, was abrupt and involved an outlet trap with a wide wooden sill leading to a 2-foot (61-cm) waterfall. These differences in configuration may account for the differences in amount of movement down the outlets of the two lakes. It is also possible that some shiners may have been resident in pools of Frye Creek itself, although no extensive areas suitable for permanent habitation were discovered.

EMIGRATION OUT OF SIXTEENMILE TOWARDS FIFTEENMILE LAKE

Evidence has been presented showing that an appreciable number of shiners move downstream from Fifteenmile Lake into Sixteenmile Lake. In the reverse direction, some of the shiners which ascended the inlet from Sixteenmile Lake probably continued on upstream into Fifteenmile Lake after spawning. Some specimens of longnose suckers, white suckers, squawfish, and rainbow trout, all of which had been marked while ascending through Sixteenmile Lake inlet trap, were subsequently recaptured by gillnet in Fifteenmile Lake. Obviously some population interchange of these four species did occur between the two lakes. No marked redside shiners were found amongst samples netted from Fifteenmile

Lake, but this may be attributable to the small number of marked fish present in proportion to the whole population. Marked shiners were however taken half way between the two lakes, immediately below a culvert which probably formed a block to upstream movement only at very high or low discharge. Adult shiners were seen at intervals along the stream both above and below this culvert, so two-way interchange of fish between the lakes probably did occur at suitable water levels.

Over two-thirds of the shiners which ascended through the Sixteenmile Lake inlet trap in either 1956 or 1957 failed to reappear as descenders. Their disappearance might have been due to death in the stream rather than to their having gone on up into Fifteenmile Lake. However, survival of some of these fish is evidenced by the reappearance the following year (Fig. 10, Table II) of 21 such fish descending through the inlet trap and bearing 1956 marks but no 1957 marks. Whether these fish overwintered in Fifteenmile Lake, or, as seems much less likely, in pools or other portions of the watershed of Frye Creek, is uncertain. However, these marked fish are direct evidence of the two-way interchange of adult shiners between Sixteenmile Lake and some upstream area.

SEX RATIO OF SPAWNERS

The following features of sex ratio, considered on an annual basis, may be distinguished in Table II: (Differences in sex ratio and size between different periods of the *same* year are considered later.)

(*h*) Amongst fish originating from Sixteenmile Lake, male ascenders outnumbered females in both years (63% males in 1956, 56% in 1957).

(*i*) The proportion of those inlet ascenders (which had originated in Sixteenmile Lake) which were recaptured as marked descenders did not differ appreciably between the sexes. Therefore, because of the unequal sex ratio amongst the ascenders (*h*), there was a larger net loss of males than of females from the lake. In 1956, 461 males and 260 females which had passed upstream did not return that year.

(*j*) Amongst fish which ascended from Sixteenmile Lake in 1957 and then returned downstream, a large proportion re-entered the inlet a second time in the same year. The propensity to reascend in this way was evidently greater amongst males than females. However, determination of the sex of this group of fish was unreliable, as is demonstrated by the recording in 1957 of more marked male reascenders (568) than had been previously returned to the lake (462). Probably some reascending females which had previously laid part of their eggs and consequently lacked the distended flanks of a fully ripe female were mistaken for males. Nevertheless, observation of the spawning behaviour of this and other species supports the view that more males than females returned to the spawning area two or more times during one season.

(*k*) In 1956, of the large number of shiners which moved downstream apparently from Fifteenmile Lake, the majority (68%) were females. In 1957 fewer such new fish moved down, and the proportion of females (44%) was much lower. The proportion of these which reascended the stream was low, but was greater amongst males than females in both years.

SIZE DISTRIBUTION OF SPAWNERS

In Table II, which summarizes available data on size distribution of shiners caught in the inlet trap, the numbers in parentheses indicate the percentage of fish in particular categories which were "large" (i.e. longer than 109 mm fork length). All fish taken in the inlet trap in 1956 were measured, except during the period from June 10 to 24 when only 26% of the fish were measured, although all were sexed and recorded as either clipped or new. In Table II and in Fig. 9 and 11, size distribution of all fish handled during this period has been assumed to be similar to that of the measured sample. Shiners were not measured in 1957, except for the sample shown in Fig. 9.

The following features of size distribution of inlet spawners may be seen from Table II:

(*l*) Females averaged larger than males in all categories shown.

(*m*) Return downstream in 1956 of fish previously marked as ascenders was higher amongst large than amongst small fish. This was true for both sexes, in each of which the proportion of large fish was about twice as great in marked descenders as in ascenders. (In both categories, however, the proportion of large fish was much higher amongst females than males, as stated in (*l*) above.)

(*n*) Of the fish described in (*m*), which ascended the inlet and then returned to the lake, some reentered the inlet a second time. These few reascenders included a disproportionate number of small fish; in both sexes the percentage of large individuals was much less amongst reascenders than amongst the group of descenders from which they had been drawn.

(*o*) New descending females (probably originating from Fifteenmile Lake) averaged significantly larger than new ascending females (originating from Sixteenmile Lake) (Table II, Fig. 9). Males in these two categories did not differ appreciably in size.

(*p*) Figure 9 shows that, as would be expected, fish marked in 1956 and recovered as second spawners in 1957 averaged considerably larger than unmarked 1957 spawners.

SEASONAL CHANGES IN 1956 SPAWNING RUN COMPOSITION

The following points regarding changes in size distribution in different periods of the 1956 inlet spawning run are evident from Fig. 11:

(*q*) A progressive decrease in average size occurred throughout the season. The decrease was greater amongst descenders than ascenders, and greater amongst females than males.

(*r*) Amongst descenders of both sexes, the proportion of marked fish decreased from the first to the last half of the season, despite the continued build-up in the numbers of ascenders which had been marked and placed above the trap.

(*s*) Size distribution of the marked descenders (stippled, in Fig. 11) tended to resemble that of unmarked descenders for the same period, rather than that of the ascending group from which they had been drawn. (In Fig. 11, the

apparent recovery of some large male descenders during June 10–23 which are not shown as previous ascenders is attributable to the measurement of only 26% of both ascenders and descenders in this period).

(*i*) Amongst ascenders, the low proportion of females (see (*h*) above) was due to paucity of females in the early half of the season. In the late half females slightly outnumbered males. Sex ratio amongst new descenders did not vary much throughout the season.

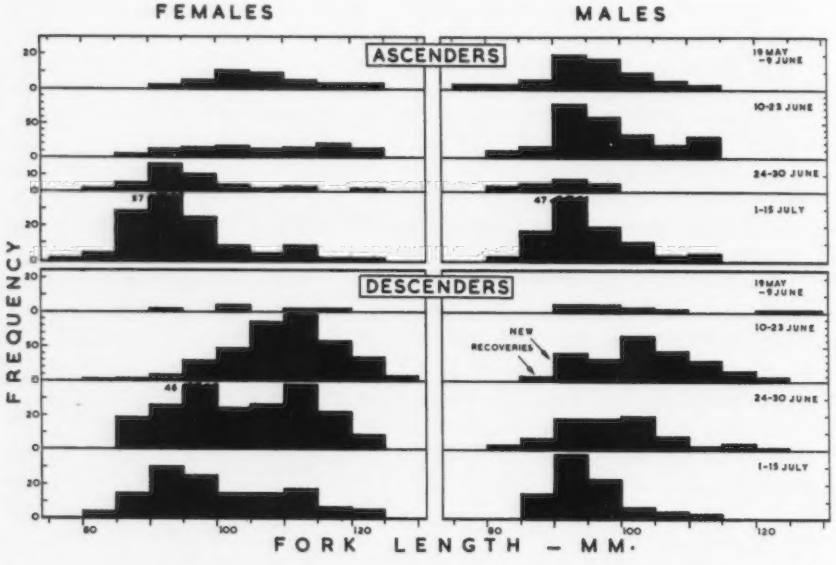

FIG. 11. Seasonal changes in length–frequency distributions of female (*left*) and male (*right*) shiners moving through inlet trap upstream (top) or downstream (bottom), in 1956. The period June 10–23 has been adjusted for incomplete sampling. Descenders include recoveries (*stippled*) which had been marked while ascending previously, and new fish (*black*) which had probably come from Fifteenmile Lake.

RE-ENTRY INTO SPAWNING STREAM

Some fish which had ascended through the inlet trap and later descended towards the lake re-entered the stream a second time during the same season (see (*f*) and (*j*) above). Because individual fish could not be distinguished, it is not known whether certain individuals may have repeatedly re-entered during the year. Some generalizations can be made however on the basis of the total numbers of recoveries of marked fish of different categories.

Despite some errors in determining sex of partly-spent fish (see (*j*) above), in most categories females probably showed less tendency than males to re-enter the stream. Usually females descending through the trap were flaccid and contained few ripe eggs; probably most of these had completed egg deposition

for the year. Occasional ripe females still distended with eggs were taken in the descender trap; these may have returned downstream immediately after being removed from the ascender trap, fin-clipped and placed upstream of the trap. The largest number of ripe female descenders was recorded shortly after the principal spawning run had commenced; females at this time may not have been fully ready to spawn and may have dropped downstream temporarily due to the onset of slightly less favourable conditions such as light or temperature in the stream, or simply as a result of handling and marking. During most of the run, however, few females re-entered the stream.

In contrast, a high but variable proportion of males re-entered the stream throughout the spawning season. Probably, like squawfish and white suckers, the redside shiner males enjoy a prolonged period of sexual activity and may revisit, or remain at, the site of spawning for many days. The fact that 2 or more males frequently accompany the spawning of 1 female in many species of suckers and minnows suggests that males commonly spawn several times during one season.

In all comparable categories of shiners (grouped according to sex and place of origin), more re-entry occurred in 1957 than in 1956 (Table II, Fig. 10). This may be associated with the much earlier spawning in 1957 (Fig. 4), when fish first entering the stream perhaps included a higher proportion of individuals not yet fully ripe.

In both years there was a much higher proportion of reascending fish amongst those which originated that year from Sixteenmile Lake (and which had already ascended through the trap once and then moved back down) than amongst those which had moved downstream from Fifteenmile Lake. A relatively high proportion of the latter type of fish were not spent when they first descended through the traps, so their failure to reascend in appreciable numbers is perhaps surprising. However, as has been suggested previously, many of these Fifteenmile Lake fish may have entered the stream accidentally or in pursuit of food, and were not necessarily close to spawning condition when first captured moving downstream.

REPEAT SPAWNERS

The term "repeat spawners" is used to imply fish spawning in two or more successive years, as distinct from the phenomenon of return to the spawning area more than once in one year, referred to previously as "re-entry". In Fig. 10 the 5 lines running between the 1956 and 1957 blocks trace the history of fish known to be repeat spawners in 1957. The sexes of most are available from Table II.

A total of 21 fish with 1956 marks first appeared in the inlet trap in 1957 as descenders, having overwintered upstream probably in Fifteenmile Lake. Of these 21 fish, 17 were males, a sex ratio very different from the unmarked fish descending through the trap in 1957 (only 56% males), but more in keeping with the preponderance of males amongst those fish which had gone upstream the year before and failed to return (see (*i*)). In fact the percentage survival

of these fish overwintering upstream was twice as great amongst males as amongst females, which further contributed to the very uneven sex ratio.

Of 268 fish which originated in Sixteenmile Lake in 1956, ascended the inlet and subsequently descended again to the Lake the same year, an estimated 123, or 46%, returned as repeat spawners in 1957. In contrast, of 797 fish which had probably originated in Fifteenmile Lake in 1956 and were first marked descending the inlet that year, only an estimated 60, or 8%, returned in 1957. (Separation between the two types is not exactly known, as distinctive marks were not applied until some time after start of operations in 1956. Allocation of some ambiguous marks have been made in Fig. 10 and Table II on the basis of the behaviour of fish with known 1956 origins.) Perhaps, of these 2 categories of fish, those which had originated in Fifteenmile Lake in 1956 showed a higher mortality over winter because they were on the average larger and presumably older (see (*o*) above). Perhaps on the other hand, having originally moved *down* the outlet of Fifteenmile Lake, they had less propensity to *ascend* an inlet stream at spawning time the following year. This is in keeping with the suggestion from other data (*see* Homing) of a heightened tendency for repeat spawners to return to the inlet creek if they had spawned there previously.

Return in 1957 of fish which disappeared upstream in 1956 was only 3%. Upstream passage from Sixteenmile Lake to Fifteenmile Lake was blocked at low water by a culvert, so late ascenders may have been delayed for some time in shallow pools offering little cover. Predation by mink was known to occur; these and other predators may account for low return of shiners which either made the two-way passage between the lakes or overwintered in the stream. Winter mortality may have been higher in Fifteenmile than in Sixteenmile Lake because of shallower depth and lower flushing rate. In addition, fish which ascended the inlet of Sixteenmile Lake in 1956 may have shown less tendency to move down the outlet of Fifteenmile Lake in 1957; by doing so, although they would be re-entering the same stream, they would be displaying an opposite current reaction at spawning time. Whatever the explanation, the percentage survival to reappear as repeat inlet spawners in 1957 was only 3% amongst marked fish which had been placed above the trap the previous year, as against 18% amongst marked fish overwintering below the trap.

HOMING

Information is not available concerning the return of spawning shiners to the stream of their own genesis ("reproductive homing" of Lindsey *et al.*, 1960), because fry were not marked at their first entry to the lake. However, it was possible to study "homing" in the much looser sense of the propensity of a fish to return in successive years to its site of previous spawning.

Fish entering Sixteenmile Lake from either inlet or outlet stream were distinctively clipped in 1956 and 1957, and samples of spawners were examined in these two streams in 1956, 1957, 1958 and, in the inlet only, in 1959. The site of capture was recorded as either "home" or "stray" depending on the site

of marking one or more years previously. Marking, and sampling, was much more concentrated at the inlet in all years. All available data were lumped in a single chi-square analysis to overcome the very uneven number of fish marked, and sampled, at the two streams. Table III shows combined results of assorted trap catches and seine samples from 1957 to 1959, and includes only fish believed to have been marked as spawners one or more years previously. Year of marking on a few of these was questionable; such fish have been classed so as to lessen

TABLE III. Numbers of shiners recaptured spawning second or subsequent times, classified by recapture site and by place of marking in a previous year or years.

	Marked in inlet	Marked in outlet
Recaptured in Inlet	192	13
Recaptured in Outlet	1	2
Chi-square = 8.35, P = 0.01–0.001		

the likelihood of significant "homing". Nevertheless, calculation of chi-square (with correction for small sample size in some cells) indicates a significant tendency ($P<0.01$) for marked fish to return to the stream of their previous spawning.

In the foregoing calculation recaptures during the year of first marking (*see* "Re-entry into spawning stream") were omitted. The large amount of re-entry into the inlet in 1957 (Fig. 10), primarily by males, produced in that year a highly significant tendency towards short-term "homing" ($P < 0.001$). On the other hand, chi-square analysis of site of recapture in 1956 of fish marked the same year demonstrated no significant tendency to re-enter the stream of first capture in that year ($P > 0.10$). Almost all "strays" in each year were fish which originated *below* the outlet trap, ascended into Sixteenmile Lake and then moved on up the inlet the same year (Fig. 10).

Evidently, although spawning shiners in Sixteenmile Lake favour the stream of a previous year's spawning, there is an appreciable amount of straying between inlet and outlet, as well as between Sixteenmile Lake and Fifteenmile Lake. The moderate "homing" tendency is apparently not stringent enough to allow the existence of genetically discrete races within the lake.

ANAL FIN RAY COUNTS

Because in this species the number of anal fin rays is known to be subject to environmental modification, ray counts of samples of shiners from the two lakes were compared for evidence of population segregation. Counts in each lake varied widely, and no significant difference was found between the means of Fifteenmile and Sixteenmile Lake samples (Table IV). As in other localities having high mean anal ray counts (Lindsey, 1953), females in both lakes had significantly higher counts than had males.

TABLE IV. Anal fin ray counts of redside shiners.

Lake	Sex	16	17	18	19	20	21	22	Mean
Sixteenmile	♂	2	2	14	5	3	0	0	18.19
	♀	1	2	8	10	2	2	0	18.64
Fifteenmile	♂	2	6	1	5	0	0	1	17.93
	♀	0	6	13	13	13	2	0	18.83

The temperature to which shiner eggs were subject in the inlet was known in 1956 and 1957 to range from about 9° to 25° C, with means of 12° to 15° for a large part of the incubation period of most eggs (Fig. 4). Fry moved downstream to the lake before the anal fins were visibly developed (Fig. 2), so ultimate fin ray count may have been affected by lake temperatures. In 1957, during the time fry were entering the lake, water temperatures at the outlet surface ranged between 13° and 25° (means between 15° and 20°), and may have been higher in protected sunlit shallows.

Because of uncertainty as to the temperatures actually effective during fin ray formation here, the data cannot be used to resolve the apparent conflict between the positive association between temperature and ray count found in British Columbia (Lindsey, 1953) and the negative association found in Montana (Weisel, 1955). Sixteenmile Lake fish have higher mean ray counts than any locality examined in either previous study, while the recorded lowest mean and minimum temperatures in Sixteenmile are well *above* those recorded in any of Weisel's localities. However, Sixteenmile Lake is also one of the most northerly populations of redside shiners studied, and latitude appears generally to be positively associated with ray count in this species. Finally, the fry leaving Frye Creek evidently undergo quite a temperature change; meristic counts are known to be sometimes subject to more modification by changing than by sustained temperature.

DISCUSSION

The role of environmental factors in inducing migrations associated with rainbow trout spawning has been made a subject of speculation by Hartman *et al.* (1962). Present data on redside shiners also suggest correlations between certain environmental changes and timing of migrations, although again no direct causality can be proved. Time of first entrance of adults into the inlet spawning stream varied markedly from year to year, and showed a close correlation with the date at which creek temperatures first exceeded 10°C (Fig. 5). No correlation with water level was observed. Throughout the protracted spawning season surges of upstream movement were associated with periods of rising water temperature, but not with water level changes. Limited observations showed the time of entry into the inlet stream each day to be restricted

largely to afternoon and evening (Fig. 6). Egg deposition seemed to occur sporadically during either daylight or darkness.

Northcote (1962) showed that downstream movement of rainbow trout fry in inlet streams occurred by downstream displacement during darkness. Similarly in redside shiners downstream movement of fry in the inlet occurred mostly during darkness, and more markedly on an overcast than on a moonlit night (Fig. 8). Daily catches of descending fry were greatest after rainy periods when the stream was both high and turbid (Fig. 7). Unpublished data on downstream movement of sucker fry in the same stream also showed a marked association between downstream displacement and darkness. Moreover, hanging a gasoline lantern over the water upstream of the trap at night caused a striking reduction in the number of sucker fry moving down. (This experiment was performed too early in the season to test the reaction of shiner fry.) Probably in all these cases downstream displacement is associated with loss of visual orientation. Displacement might be modified or prevented if the fish maintained tactile contact with the bottom, or sought quiet water amongst stones or at the stream margin. Northcote (1962) has shown in trout that these responses vary at different temperatures, different photoperiods and different fish sizes. Such information is lacking on redside shiners, but the net result of environment and behaviour is evidently to displace most or all of the shiner fry out of the inlet creek and into Sixteenmile Lake soon after hatching. This probably has the dual advantage of removing them from a habitat which is exposed and, in dry years, ephemeral, and also of transporting them to a habitat where food (presumably plankton) is more abundant.

Many facets of the Sixteenmile Lake shiner population, involving numbers, size, sex distribution, and movements, have been described and need not be reiterated. The picture which emerges is that of a somewhat sparse, rather stable population with what appear, for small "minnows", to be surprisingly low rates of recruitment and of death. The density of adults is only about 300 per acre (750 per hectare), probably well below that of other lakes (Paul, Pinantan) which have been studied. However, the lakes are not strictly comparable, as Sixteenmile Lake has stained water, total dissolved solids of 60 parts per million, and oxygen deficiency except in the upper few feet (2–3 metres), and also contains 4 other species of larger fish to share the available food. Some shiners in Sixteenmile Lake probably live 6 or 7 years, and many survive to spawn in 2 or more successive years. Population interchange between Sixteenmile Lake and waters tributary to the inlet creek can evidently be extensive and subject to annual variation.

The fate of eggs laid in Frye Creek by shiners moving down out of Fifteenmile Lake is unknown. Newly emerged fry are probably incapable of ascending the swifter parts of the creek, and quite possibly all fry emerging in Frye Creek between Fifteenmile and Sixteenmile Lake are swept down into the latter. Older shiner fry or fingerlings are rarely, if ever, seen in the creek in mid summer

or autumn. If so the population in Fifteenmile Lake may be maintained by the occasional upstream movement of adults from Sixteenmile Lake (such as occurred in 1957), or by spawning in the short swampy outlet of Fifteenmile Lake, or by lake spawning.

Whether or not lake spawning occurs in either lake has not been determined. Sixteenmile Lake contained about 13,000 adults, yet the number captured in the traps was only about 2200 in 1956 and 5000 in 1957. However, at low water some egg deposition was known to occur in the creek mouth within a few feet of the lake, and considerable spawning may have occurred in the delta of the inlet below the inlet trap. Also, adult shiners may not always spawn each year. Thus there may or may not be extensive lake spawning in this lake.

Almost certainly lake spawning by redside shiners does occur in some lakes having no appreciable drainage, and in others where young fry have been taken remote from either inlet or outlet creeks. As shiners in different areas are evidently capable of reproducing in standing water, in inlet streams or in outlet streams, the question arises as to what determined their spawning sites in the system under discussion. In Fifteenmile Lake at least a portion of the fish move down the outlet to spawn; in Sixteenmile Lake almost no outlet spawning occurs, and of two inlets, Frye Creek and Muggins Creek, only the former supports spawning, although the two do not differ markedly in temperature.

These observations do not suggest a single set of environmental requirements (certain combination of temperature, water flow, etc.) which act as "releasers" of spawning in both lakes. An alternate view is that differences in innate preference for certain spawning conditions have been produced in the two different populations by sharp selective pressures. Because offspring of shiners spawning in Sixteenmile Lake outlet stand little chance of surmounting a beaver dam to regain the lake, there may have been selection against outlet spawning. However, interchange of adults between the two lakes seems too great for marked genetic differences to be maintained between the two populations.

Instead, choice of spawning site may be dictated by a rather strong tendency for shiners to "home" to the stream of their own genesis, using learned cues perhaps involving olfaction or vision. Once there, spawning may occur over a wide range of environmental conditions. Thus, the allocation of spawners amongst the various possible types of spawning ground (inlet streams, outlet, or lake shore) may in each lake reflect the relative success of reproduction in each of these areas during the past few generations. Marking has demonstrated a moderate degree of straying such as would enable a population to expand fairly rapidly to exploit a newly available spawning site. The very small numbers of fish entering Muggins Creek or the Sixteenmile Lake outlet may be due to frequent early drying up of the former and a block to upstream passage in the latter, rather than to anything intrinsically "unattractive" about either stream. Perhaps few fish enter these streams simply because they are "home" to few fish.

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Temperature, Salinity and Plankton in the Eastern North Atlantic and Coastal Waters of Britain, 1957. II. The Relationships Between Species and Water Bodies[1]

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ABSTRACT

Occurrences of seventeen species of zooplankton from near-surface oceanic and coastal waters about Britain have been correlated with temperatures and salinities, in temperature-salinity-plankton (T-S-P) diagrams, for the 12 months of 1957. Species exhibit distinctive relationships to the several water bodies, as these have been defined in temperature-salinity (T-S) diagrams. Similar relationships between species have been used as a basis to group species together and 6 such groups are discussed. The species of three of the groups are oceanic; one of these groups is restricted to warm water, but the others are less restricted. A fourth group consists of species confined to coastal waters. The remaining two occur in oceanic, mixed oceanic-coastal and coastal waters. The relationships to the water bodies are shown to persist throughout the seasonal fluctuations of properties in the waters.

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INTRODUCTION

TECHNIQUES have been developed which directly relate occurrences of species to bodies of water characterized by temperatures and salinities in temperature-salinity (T-S) diagrams. Pickford (1946, 1952) first used the technique and showed that a cephalopod, *Vampyroteuthis infernalis* Chun, occurred in the Indian Ocean in Indian deep water and lower levels of Indian equatorial water, and in the Atlantic, in the deep water and deep South Atlantic Central water. Since then Haffner (1952) with the bathypelagic fish *Chauliodus*, David (1955, 1958) with Chaetognatha, and McGowan (1959) with an aberrant pelagic polychaete *Poeobius*, have shown relationships of species to water masses.

In these investigations the presence of a species, and sometimes its relative abundance, was symbolised either in the intercept of temperature plotted against salinity, or against the T-S curve, for the positions at which it was collected. They have demonstrated that occurrences of species coincided with the presence of particular oceanic water masses depicted in the manner of Sverdrup *et al.* (1942).

For depths greater than about 100 m the conventional T-S diagram represents relatively permanent conditions. Because this is so, separate series of observations on hydrography and occurrences of species may be combined whenever required.

In coastal waters, and the upper tens of metres of the ocean, fluctuations, or less regular variations of temperature and salinity are caused by seasonal climatic influences, or runoff, precipitation and evaporation. In circumstances such as these the modified T-S diagram introduced by Miller (1950) and adapted by Rochford (1957) and Bary (1959, 1963) enables the surface waters to be investigated. The addition of occurrences of species to this type of diagram produces the temperature-salinity-plankton (T-S-P) diagram (Bary, 1959).

Neither the technique for deep nor that for surface waters has been used to follow the relationships between species and water bodies continuously over a prolonged period, although David (1955) demonstrated a change in depth between winter and summer for the Antarctic chaetognath, *Sagitta gazellae* Ritter-Zahony. In the following account, monthly plankton data for 1957 are analysed in relation to the several "bodies" of water characterised (Bary, 1963) from the eastern North Atlantic, North Sea and English Channel. (A surface T-S diagram typical of those of Bary (1963) is shown in Fig. 1.)

The T-S-P diagrams have enabled environmental relationships of 17 species to be demonstrated. Species with similar, but not necessarily identical relationships, are grouped together.

MATERIALS

The plankton was collected from January through December, 1957, with the Continuous Plankton Recorder (CPR) (Hardy, 1939) at a depth of approximately 10 m in the course of routine surveys conducted from the Oceanographic Laboratory of the Scottish Marine Biological Association. In Fig. 2, the positions are indicated of the commonly sampled routes in the North Sea, and westward of

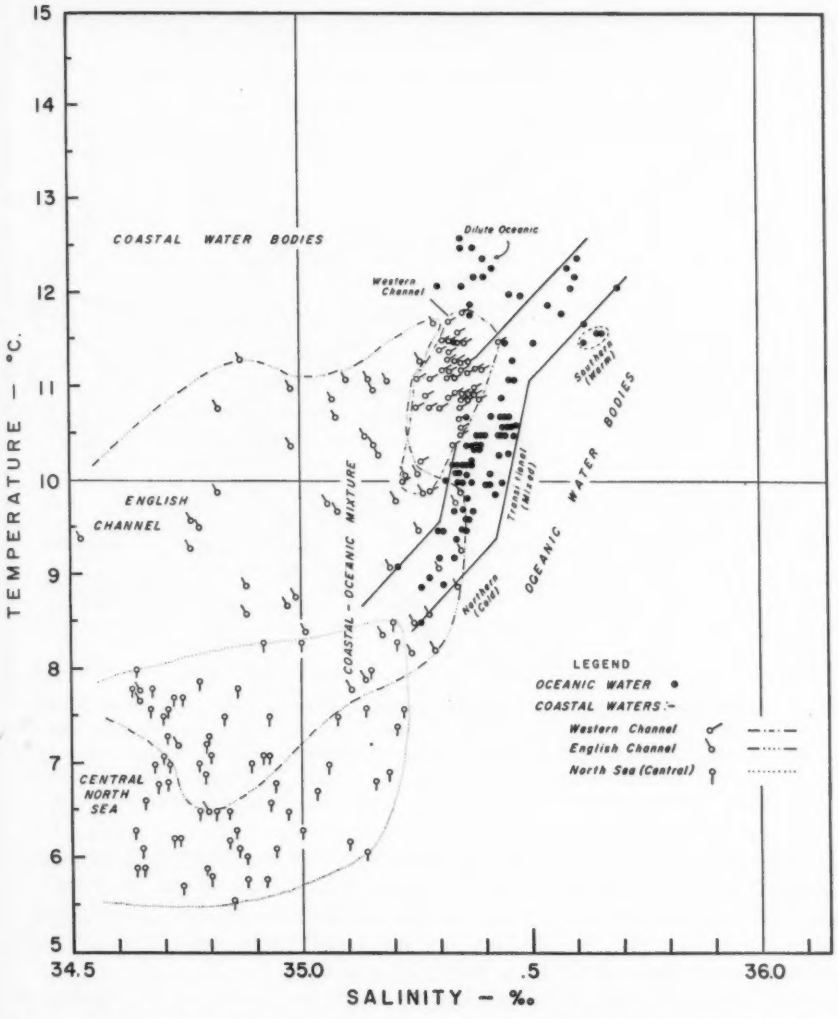

FIG. 1. Typical T-S diagram of surface waters of the eastern North Atlantic oceanic and coastal areas of Britian. This diagram is a slightly modified version of that presented for January by Bary (1963).

Britain. The routes running approximately north-west and south-west from Northern Ireland were more numerous than shown; those entered illustrate the areas covered during the year. Routes additional to those shown in Fig. 2 were sampled, but data from them could not be used because concurrent hydrographic observations were not made: areas to north and south in the oceanic region, and much of the North Sea, are affected (see John and Brown, 1958, for all routes sampled during 1957).

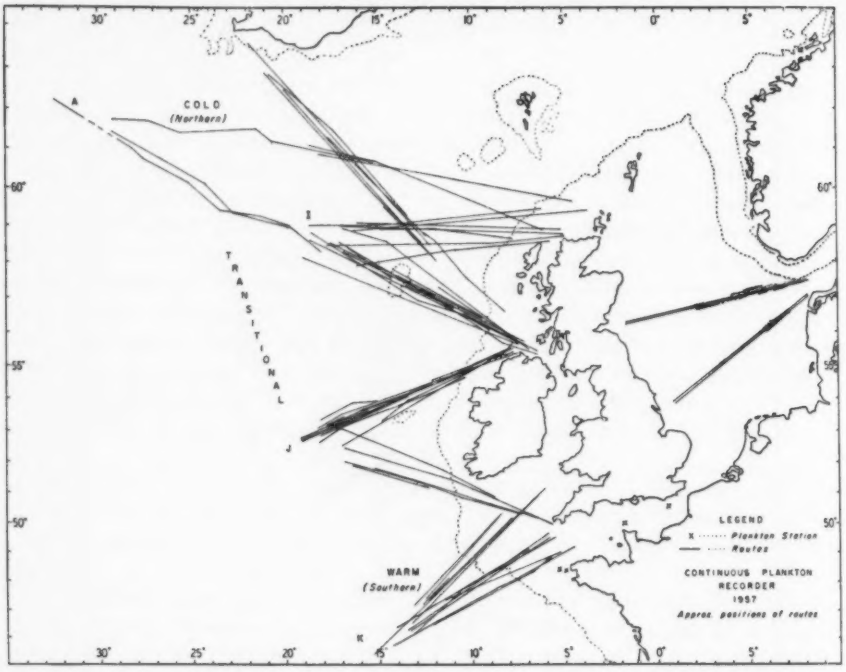

FIG. 2. Generalised diagram showing approximate locations of the Continuous Plankton Recorder routes used in the present study. In the North Sea only the positions of the two regularly sampled routes are shown; some routes extending from northern Ireland are excluded for clarity. Not all routes were sampled during each month; "northern", "transitional" and "southern" refer to the general areas occupied by the water bodies discussed in the text.

The analysis of CPR collections has been detailed by Hardy (1939), Rae and Fraser (1941), and Colebrook (1960). The "eyecount", and the "traverse" of the CPR silk with the aid of a microscope, provide data for making comparable estimates of the numbers respectively of larger and smaller organisms. A scale of relative abundance is shown on each of Plates I to IX.

In Table I the species included in the study are listed and the method of enumeration (by "traverse" or "eyecount") stated.

Species are individually symbolised in all diagrams.

The water envelopes used are reproduced from Bary (1963).

PROCEDURE

In constructing the T-S-P diagrams (Bary, 1959) the relative abundance of a species collected at a particular location is entered, using symbols, in the intercept of the temperature and salinity at that location. This is repeated for all stations occupied in an area. Occurrences and relative abundances of species are thus correlated with the hydrographic conditions, exemplifed by temperature

TABLE I. Species of zooplankton included in the study, their groupings and the type of analysis employed in their enumeration.

Grouping and species	Animal type	Type of analysis*
Warm (southern) group:		
Centropages bradyi	Copepod	E
Euchaeta tonsa	Copepod	E
Euchaeta acuta	Copepod	E
Nannocalanus minor	Copepod	E
Warm-transitional group:		
Pleuromamma robusta	Copepod	E
Pleuromamma gracilis	Copepod	E
Sagitta serratodentata	Chaetognath	E
Cold (northern)-transitional group:		
Pareuchaeta norvegica	Copepod	E
Warm-transitional-neritic group:		
Euchaeta hebes	Copepod	E
Candacia armata	Copepod	E
Centropages typicus	Copepod	T
Spiratella retroversa	Mollusc	E
General-neritic group:		
Metridia lucens	Copepod	E
Acartia clausi	Copepod	T
Coastal (neritic) group:		
Temora longicornis	Copepod	T
Sagitta elegans	Chaetognath	E
Sagitta setosa	Chaetognath	E

*E = relatively large organisms the numbers of which were estimated by "eye"; T = relatively small organisms the numbers of which were estimated from a count made during a traverse of the Continuous Plankton Recorder silk with the aid of a microscope.

and salinity, for the times and places at which the species were collected. It is essential for near-surface T-S-P diagrams that plankton and hydrographic data be collected concurrently since fluctuations in occurrences of species and distributions of water properties may be frequent and rapid. This is especially important at or near fronts and in mixing waters.

Only data from brief periods should be used in any one T-S-P diagram. The rate of change in temperature of near-surface waters, as a result of seasonal climatic fluctuations, is of chief consideration. If a large, rapid change, or too long a period was encompassed in one diagram, the occurrences of a species might appear to extend into waters to which it did not belong. In the present study, each T-S-P diagram includes data from one calendar month.

Only organisms identified with reasonable certainty are useful in T-S-P diagrams. In the present study these are mainly copepods, but three species of chaetognath and one pelagic mollusc were also available. One copepod, *Acartia*, was not identified to species, but frequent checks have shown that species other than *Acartia clausi* are rare in the CPR collections (Colebrook *et al.*, 1961a; Colebrook *et al.*, 1961b). Similarly, *Candacia* is regarded as *C. armata*.

Other organisms, for example those analysed at the generic level such as *Calanus* spp., but known to be multi-specific, and species in one or two other categories have been excluded. Chaetognaths in the North Sea were analysed only for November and December of 1957.

The correlation of plankton data with hydrographic observations presented difficulties. Firstly, the CPR was towed at approximately 10 m depth, but temperatures and salinities were observed between 0 and 5 m. Secondly, only alternate sections of silk were analysed. Thirdly, plankton representing the collection from 10 mi of towing has been plotted in the intercept of the temperature and salinity observed at a "point" lying somewhere along the 10-mi tow. And fourth, one or a few of the analysed silk sections were occasionally out of phase with the hydrographic observations. However, if the temperatures and salinities indicated relatively uniform environmental conditions (i.e. variations within 0.5 ‰ and 0.5 C°) over the distance represented by the sections of silk, the location of one or more of the sections was either advanced or retarded by a distance of 10 mi. If uniformity did not exist, the plankton data were discarded. The factors outlined possibly have contributed towards some generalisation in the relationships between the species and water bodies, but in the broad approach imposed by the sampling method and analysis procedure this has not been obvious and has probably had little effect.

Bary (1959) briefly discussed diurnal vertical migration in relation to the T-S-P diagram. He stated that although details would be affected, in general the occurrences of species in day tows supplemented those taken at night because the species were usually present only in those water bodies with which they had been associated in the diagram. In other words, the total occurrences of a species, including its abundance, determines the environmental conditions (water body or bodies) with which it will be associated by means of the T-S-P diagram.

In the present survey the water bodies usually were extensive, and day and night sampling in them was fairly random. A diurnally migrating organism may have been absent from some stations during daylight, but it could well have been collected from the same water body during the night and therefore be adequately represented in the T-S-P diagram. For small pockets or intrusions of water, a "smoothing effect" resulting from the methods of sampling and analysis, usually would mask a change in the fauna. Relationships between species and the environment may not be demonstrated in such cases.

It must be emphasised that interpretations and conclusions in the present study are concerned with trends apparent during the whole period being reviewed; particular months are used as examples in discussions.

GROUPING OF SPECIES

The relationships shown in the T-S-P diagrams between species and water properties have been used as a basis for classifying the species. Similar relationships enable species to be grouped together. Consistent differences between one group and another set them apart. The groups are named according to the conditions in which the constituent species occurred (Table I).

Six groups have been delineated. The warm (southern) group of four species of copepods was restricted to the southern water body; the warm-transitional group, two species of copepod and one chaetognath, extended between southern and transitional waters, and the northern (cold)-transitional group, only one species of copepod occurred in northern and cooler transitional water. The species of these three groups were almost entirely oceanic in their occurrences. The species of the coastal (neritic) group, were collected almost only from water of coastal properties, or a mixture of coastal and oceanic waters. The two remaining groups consist of species which occurred in oceanic and mixtures of oceanic and coastal waters. The groups and the species are listed in Table I.

Because concurrent CPR collections and hydrographic observations were not available from waters to the north of the area being considered, northern species such as *Metridia longa*, *Calanus hyperboreus* and perhaps *Eukrohnia hamata*, (Fraser, 1952) have had to be excluded.

Warm (Southern) Group: Plates I to III

Species in the group are the copepods *Centropages bradyi* Wheeler, *Euchaeta* (*Pareuchaeta*) *tonsa* Giesebrecht, *Euchaeta acuta* Giesebrecht and *Nannocalanus minor* Claus.

In the T-S-P diagrams all four species were entirely oceanic in their relationships and restricted to the southern water body, except for a few specimens of one or more of the species present in transitional water in September, October and November. Specimens were collected during February, March and September, from low-salinity water. This water was interpreted (Bary, 1963) as being of oceanic origin and occurrences in it of species with close affinities to oceanic water support this. The species also occurred in pockets of high salinity, oceanic water, e.g. February. Therefore, they were tolerant towards a wider range of salinities than was present in the southern water for the months concerned.

The close association between the species and the southern water body was maintained throughout the summer rise in temperature, and during the early part of the cooling cycle (September and October), when sampling was adequate and the species were present. They disappeared during November and December, although the mean temperature of southern water (Bary, 1963) was higher than in the previous February when the species first appeared.

No interspecific differences were detected in relationships to the southern water body. This probably is because the species were scarce and the monthly series was incomplete; in addition the species fluctuated in abundance (January to March; July and August) which made the detection of such differences difficult.

Warm-Transitional Group: Plates IV to VI

Species in the group are *Pleuromamma robusta* (Dahl), *P. gracilis* (Claus), both Copepoda, and *Sagitta serratodentata* Krohn (Chaetognatha). The "forms" of *S. serratodentata* have not been identified; both *S. s. tasmanica* Thomson, and *S. serratodentata*, may have been present (Fraser, 1952: Furnestin 1953).

The number of specimens and the frequency of occurrences of *P. robusta* and *P. gracilis* during February, March, August, and perhaps December, was highest in southern water. *Sagitta serratodentata* was not collected during the 6 months of January, February, April, May, June or August. It was present during March and December in southern water, without contemporaneous occurrences elsewhere; in November specimens were collected from southern and transitional water. During July, September and October *S. serratodentata* was present in transitional water, but sampling was not adequate to show whether it occurred in southern water.

The occurrences of *Pleuromamma* spp. and of *S. serratodentata* suggest they originated in southern water and dispersed from there into transitional water. Unfortunately data were too few from April to June and from September to November to indicate a southern water origin for *P. robusta* or *P. gracilis*; in July specimens were absent from southern water. However, occurrences of *S. serratodentata* complement those of *Pleuromamma* over these months.

The warm-transitional group was restricted to oceanic waters, except for an occurrence of *P. robusta* in October in water of possible coastal origin. Specimens were present in pockets of high-salinity oceanic water (February). They also occurred during January to March, and in September in low-salinity water. As with the previous group such occurrences of species with close affinities for oceanic water support the interpretation of an oceanic origin for the low-salinity pockets.

Differences were demonstrated between *P. robusta* and *P. gracilis* in their relationships to the water bodies. *Pleuromamma robusta* occurred throughout southern and transitional waters and at times, in late autumn and winter months (January, November, December), in low numbers in northern water. *Pleuromamma gracilis* on the other hand penetrated into transitional water only to about one-half the extent of *P. robusta*, that is, to about the equivalent of a "50% mixture" of southern and northern water. *Pleuromamma robusta* also was present in higher numbers earlier and later in the year than *P. gracilis*.

Inadequate data prevent the relationship of *S. serratodentata* to the water bodies being defined; it appears to be broader than for *P. gracilis*, but less than for *P. robusta*.

The warm-transitional group maintained its close association with the southern and transitional water bodies during the seasonal increase of temperature, up to July and August. The associations with both waters probably continued from September on, when temperatures were decreasing, but the diagrams show this only in transitional water. The interspecific differences between *P. robusta* and *P. gracilis* were maintained throughout the seasonal fluctuations in the water bodies.

Cold (Northern)-Transitional Group: Plates I to III

The third oceanic 'group' consists of one species of copepod, *Pareuchaeta norvegica* Boeck.

Although a few specimens of *P. norvegica* occurred in April in cool transitional water, the species appears to have originated in northern water (May, June and

November) and extended thence into transitional water (June, August to October or November). The relationship to oceanic water is close, but it was present in October in water regarded as of coastal origin. In September two samples were collected from a pocket of diluted oceanic water.

The relationships of *P. norvegica* may be complicated by a seasonal vertical migration (Rae and Rees, 1947; Hansen, 1960). This behaviour may account for its absence during January to March and December.

The dispersal of *P. norvegica* from northern into transitional water runs counter to the movements indicated for species in the previous groups. Presumably the species are following the courses taken by northern and southern waters during mixing to form transitional water.

WARM-TRANSITIONAL-NERITIC GROUP: PLATES VII TO X

Four species are included in the group, *Euchaeta hebes* Giesbrecht, *Candacia armata* Boeck, *Centropages typicus* Kroyer (Copepoda), and *Spiratella* (= *Limacina*) *retroversa* Fleming (Gastropoda).

Candacia armata first increased in numbers in southern water (February, March, August) and dispersed into transitional water (March, June and September to December) and into oceanic-coastal water, possibly from the transitional water. The frequency of its occurrences in oceanic waters was either equal to, or higher than in oceanic-coastal waters up to September. In October and November, however, the reverse was true. There was a marked decrease in all waters in December. There were no records of *C. armata* occurring in the northern water body.

Centropages typicus was present in oceanic or oceanic-coastal waters, but in low numbers, in February, March, May and June. In July and August it became plentiful in both oceanic and oceanic-coastal waters and high numbers were maintained up to October. By November and December only a few specimens remained, mostly in the oceanic-coastal and coastal waters.

From July to October the occurrences of *C. typicus* were continuous between oceanic and oceanic-coastal waters in the T-S-P diagrams. Except for September and perhaps October, this continuity was between southern and warm transitional waters and warm oceanic-coastal water. Increases and decreases in numbers in the oceanic and oceanic-coastal waters were concurrent, although the average number of specimens per sample would appear to have been slightly higher in the oceanic-coastal water.

Centropages typicus was often present in the cooler transitional water, but only in August and September in comparatively high numbers. It was not collected from cold northern water, but it occurred in coastal water (May, November and December) at temperatures lower than those at which it was present in oceanic waters. *Centropages typicus* was generally more numerous than, but similar in its occurrences to, *C. armata*.

Spiratella retroversa was present continuously in oceanic waters from March to November; usually it was sparse, but it became relatively common in September and October. It occurred in southern water in March, April, August and October; presumably the tendency to occur in warmer transitional water (except

September) was associated with such warm-water occurrences. Specimens were not collected from northern water, although they were present in inshore waters in winter months at lower temperatures than were current in the open ocean.

Relationships of *S. retroversa* are complicated by the much higher numbers usually collected from the oceanic-coastal than from oceanic waters. Possibly the species were breeding in these waters subsequent to seeding from oceanic water, or they may have been concentrating there from depths other than sampled. Separate populations may have been sampled, but this is unlikely in view of the continuity of occurrences between oceanic and inshore waters already discussed.

The four species *Euchaeta hebes*, *Candacia armata*, *Centropages typicus* and *Spiratella retroversa* occur in the T-S-P diagrams in oceanic water, usually the southern and warmer transitional waters; except for *E. hebes*, the diagrams also show periods when occurrences were continuous between the oceanic and oceanic-coastal waters. These features seem to suggest the species were moving from oceanic into the oceanic-coastal waters, despite the higher numbers at times in the latter.

In the coastal waters there is usually an abrupt decrease in numbers of specimens of the warm-transitional-neritic group at salinities less than about 34.9 ‰. In northern European waters, salinities greater than about 35 ‰ are considered to result when oceanic and coastal waters mix (Bary, 1963). It seems, therefore, that the decrease in numbers of specimens coincides with the advent of typically coastal water.

The association between the warm-transitional-neritic species and the southern and transitional water bodies remained close throughout the seasonal fluctuations in temperature. The species were also present in coastal waters so that the range of conditions occupied was wide. Therefore the association is not as readily apparent as with the warm (southern)- or warm-transitional groups. It is pertinent to note that all except *Euchaeta hebes* occurred in coastal waters (February to April) at lower temperatures than were being experienced concurrently in oceanic waters.

General-Neritic Group: Plates XI to XIV

The group contains two species of copepod, *Metridia lucens* Boeck and *Acartia clausi* Giesebrecht.

From the T-S-P diagrams these two species are seen to occupy a wider range of conditions and to be usually more abundant than species of the warm-transitional-neritic group.

Metridia lucens occurred in relatively high numbers in the southern and warmer transitional waters in February, April and August and again, but less noticeably, from September to December. On the other hand, it was present in moderate numbers in northern water in March, May and November and in lower numbers in several other months.

From January to April, *Acartia clausi* occurred in small numbers throughout transitional water and in March in northern water as well. In May numbers increased in cool transitional water. In June, although there was a general

increase in occurrences of the species, numbers remained higher in the cool transitional water; it also extended into northern water, but was restricted to the warmest of this water. A similar situation may have persisted into July. A few specimens occurred in northern and cool transitional waters in November and December. During periods when *A. clausi* was abundant, its numbers increased in the warmer transitional water (e.g. June, August, October), but even so, it was more plentiful in the cooler transitional water. The rare occurrences in southern water (August and November) may have been stray specimens from transitional waters.

Although *M. lucens* clearly may occur over a wide range of conditions in oceanic waters, the higher numbers in February, April, August, September, and December in the southern waters suggest it originated there. Water movements may have carried the specimens in northern water in from elsewhere, or another population may have been sampled. The T-S-P diagrams do not provide information on the latter points. The oceanic occurrences of *A. clausi* indicate that it prefers the cool transitional water, but can extend into warmer transitional and northern waters.

When *M. lucens* became plentiful in oceanic waters in February, March, October and November it increased to much higher numbers in the oceanic-coastal water; on the other hand, when numbers decreased in all waters from April to June, relatively higher numbers were maintained in oceanic water. From April to May, *A. clausi* was present in oceanic waters in moderate numbers, but was infrequently collected from the oceanic-coastal water; in June and July however, the numbers increased in both waters. A subsequent decline in numbers began in the oceanic-coastal water (August, September), but did not become evident in oceanic water until September and October. There was no noticeable disparity in numbers between oceanic and oceanic-coastal waters such as occurred with *M. lucens*.

These data indicate some independence between oceanic-coastal and oceanic waters in the fluctuations of abundance of the two species. This could result from sampling separate populations in the inshore and offshore waters. For example a neritic population of *A. clausi* may occur in the North Sea (Colebrook *et al.*, 1961b). Alternatively both species were more consistently present in oceanic than in the oceanic-coastal waters, and moreover, there was frequent continuity of occurrences between the waters. These points suggest specimens in oceanic water were a reservoir for recruitment to the oceanic-coastal water. If so, the high numbers of *M. lucens* in oceanic-coastal waters in February, March, October and November may have resulted from breeding.

There was a reduction in numbers of *A. clausi* and *M. lucens* at salinities below 34.9‰ similar to that which occurred for species of the warm-transitional-neritic group. However, large samples of both species were not unusual at the lower salinities which probably indicates a less restricted relationship to the coastal water. Or again, neritic populations may have been sampled.

Acartia clausi and *M. lucens* maintained generally close relationships with the water bodies throughout the seasonal fluctuations in their properties. The

relationships are somewhat obscured by their broad nature and some lack of sampling at critical times. Occurrences of the two species in North Sea water during January to April indicate they are able to withstand cooler temperatures than they were subjected to concurrently in the open sea. At such times, numbers were relatively much lower than in either oceanic or oceanic-coastal waters.

In oceanic waters, *M. lucens* at times occurred over the whole range of conditions sampled, but it probably originated in the warmer oceanic waters. This may also apply to specimens in northern water, if they were transported in currents; or another population may have been sampled. For *A. clausi*, the evidence suggests that in its oceanic occurrences in the eastern North Atlantic it is largely confined to the cooler transitional water. Both species appear to move from oceanic to oceanic-coastal water. In the inshore waters they occurred over roughly similar conditions. *Metridia lucens*, but not *A. clausi*, was present in higher numbers in oceanic-coastal waters early and late in the year.

Coastal (Neritic) Group: Plates XV to XVII

Three species are brought together in the coastal group, *Temora longicornis* O. Fr. Muller, (Copepoda), *Sagitta setosa* J. Muller and *S. elegans* Verrill (Chaetognatha).

The species included in the coastal (neritic) group were largely restricted to the coastal, or the oceanic-coastal mixed waters. Specimens were rare in oceanic water. *Temora longicornis* was present in northern water during the unusual conditions in July (Bary, 1963); *S. elegans* occurred in transitional and southern waters in November and in oceanic water that had just begun to mix with coastal water in August and December.

Temora longicornis was not represented in samples in January, February and December. At other times it occurred over more or less the full range of conditions of coastal and oceanic-coastal waters. *Sagitta setosa* was present only once (November) at a salinity greater than about 35.1‰; conversely, *S. elegans* was not collected at salinities less than about 34.9‰, except in March and April when specimens occurred in water of 34.8 and 34.5‰, respectively. It appears, therefore that at about 35‰ salinity there was a range of approximately 0.2‰ over which *S. setosa* mingled with *S. elegans*. *Sagitta setosa* predominated at lower salinities (coastal water), and *S. elegans* at higher salinities (oceanic-coastal water). Thus, even with relatively little material, differentiation in relation to oceanographic factors was apparent. Data for the whole year from the North Sea may have broadened the range of salinities over which both *S. setosa* and *S. elegans* occurred together, but probably the general picture of differentiation would not have been changed.

DISCUSSION

Bary (1963) proposed that the surface, oceanic water bodies in the eastern North Atlantic originated in North Atlantic central water. If this is so, it would be reasonable to expect southern, transitional and northern water bodies

to be basically similar in properties, although it was pointed out that northern water may have been modified. It was of considerable interest, therefore, to demonstrate the distinctive relationships of species to these water bodies.

A high degree of specificity to particular water bodies is shown by the species of the warm (southern) and coastal (neritic) groups. The same applies to the warm-transitional and cold-transitional groups, except that two oceanic water bodies are involved. A broad relationship to several oceanic and coastal water bodies is shown by species of the warm-transitional-neritic and the general-neritic groups. But even with these, specificity is apparent in the relative restriction of species to "preferred ranges" of conditions in the oceanic and the oceanic-coastal mixture of waters, as well as their "avoidance" of typically coastal water.

Differing relationships to the water bodies among some of the constituent species of the groups have been demonstrated. For example, *Pleuromamma gracilis* usually did not penetrate into the mixed transitional water (from southern water) as freely as *P. robusta*; *Metridia lucens* more usually inhabited warmer southern and transitional water than *Acartia clausi*; in coastal water, *Sagitta setosa* was common in water at lower, *S. elegans* at higher, salinities.

The T-S-P diagrams have shown for each species that its relationships to the waters was maintained throughout the year, regardless of the temperature of the environment resulting from seasonal climatic fluctuations. Nor did the relationships of individual species towards other waters change during the year. This was most evident in the reactions of species at the boundary zones between waters—species which were not able to cross in one month usually did not cross in any month; but it also applied to the oceanic species *Pleuromamma gracilis*. The reaction of some species at a boundary zone was "immediate" in the sense that they were present on one side, but not the other; or "more gradual", when the species would penetrate into the mixed waters (oceanic-coastal and/or transitional) beyond the boundary zone. Some species (e.g. *Metridia lucens*) would seem able to penetrate further than others (e.g. *Candacia armata*) into the mixtures.

Relationships which are constant relative to the water bodies, even though these may undergo fluctuations in temperature and salinity, would seem to result from the species reacting to some other, but constantly maintained property, or properties, in the waters. If so, the relationships would not necessarily be determined by temperature and salinity. The distinct relationships within a group of species are probably due to differing tolerances to change among these species. Relationships which depend on species' tolerances would ensure that the species have the potential to be found where conditions were favourable, but not otherwise.

It seems likely that there is a wider range of relationships of species to waters in the Atlantic area than has been discussed in this study. Some "potential groupings" are illustrated in Fig. 3. Several of these are represented in the study (excluding groups originating in cold, northern waters for which there were no data), although they may be combined with species from other "potential

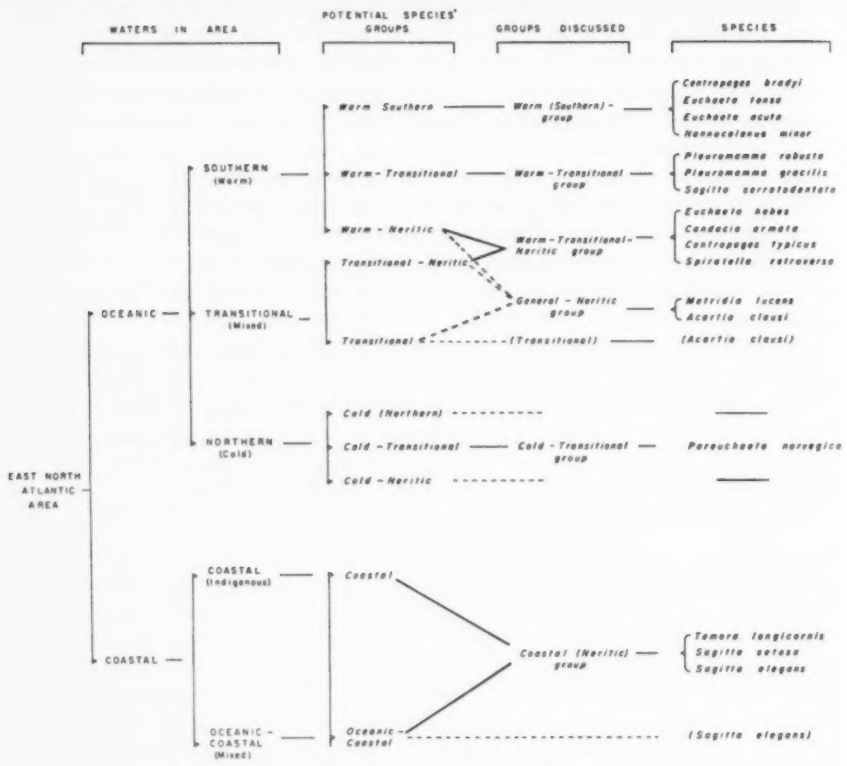

FIG. 3. Diagram indicating the waters characterised for the area surveyed and the "potential groups" of species which might be distinguished from these waters. The groups and species discussed in the paper are listed. Thick solid lines indicate probable combining in the present study of species from different potential groups; thick dashed lines indicate a suspected combining of species.

groups". Where this is believed to have occurred it is shown by thick, solid lines, e.g., the potential groups "coastal" and "oceanic-coastal" have been combined as the coastal (neritic) group. In other instances a combination of groups is suspected, and this is indicated by the thick, dashed lines.

The species of the groups discussed in this paper are also listed in Fig. 3. *Acartia clausi* and *Sagitta elegans* are listed twice, once under the group-heading used herein and once in parentheses in a designation considered to be more accurate. Clearly a more complete study than has been possible from the 1957 data would be required to fully clarify the species' relationships.

The T-S-P technique was used for surface waters about southern New Zealand (Bary, 1959). Groups of species representative of the faunas in oceanic, mixed oceanic-coastal, and coastal waters were selected in a similar manner and performed a similar function to the Atlantic groups, but contained different

species. Variations between species in their tolerances to change, of a sort parallel to those in the eastern North Atlantic, were found. Occurrences of the species enabled oceanic waters penetrating into, and mixing with, coastal waters to be traced.

The T-S-P technique therefore has provided information of a similar kind for two widely separated areas. There seems little doubt that it could be used to study species in relation to the marine environment elsewhere.

SUMMARY

1. Seventeen species of zooplankton, collected during 1957 by the Continuous Plankton Recorder from oceanic and coastal waters about Britain, have been entered on the T-S diagrams of near-surface waters presented by Bary (1963). The resulting T-S-P diagrams demonstrate the relationships of the species to the water bodies in the area. Similarity between species in their relationships has provided the basis for grouping species together.

2. Groups of species representative of the following six types of environments have been determined: warm (southern), warm-transitional, and cold (northern)-transitional waters; warm-transitional-neritic conditions, general (oceanic)-neritic, and coastal (neritic) conditions. The first three groups inhabit oceanic water bodies; the last group occurs in coastal waters; the remaining two groups occur more or less widely in oceanic and oceanic-coastal waters, but show a tendency to avoid typically coastal water.

3. Inter- and intra-specific relationships to the water bodies usually differ, but the relationships shown by an individual species varied inappreciably during seasonal fluctuations of properties (mostly of temperature).

4. General relationships to water bodies are discussed briefly.

ACKNOWLEDGMENTS

My thanks are due to Mr R. S. Glover, Officer-in-Charge, and members of the staff of the Oceanographic Laboratory, Edinburgh, for continued assistance. I am grateful to members of the staff, Institute of Oceanography, University of British Columbia, Vancouver, B.C., for their interest in and discussion of numerous points.

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PLATES I TO XVII

T-S-P diagrams showing various groups of species in relation to water bodies of the eastern North Atlantic and coastal areas of Britain for each month of 1957.

Plates I to III	:	Warm (southern) group. Cold (northern)-Transitional group.
Plates IV to VI	:	Warm-transitional group.
Plates VII to X	:	Warm-transitional-neritic group.
Plates XI to XIV	:	General-neritic group.
Plates XV to XVII	:	Coastal (neritic) group.

LEGEND TO PLATES

WARM (SOUTHERN) GROUP

Centropages bradyi ..... (E)* — △

Euchaeta tonsa ..... (E) — ⊘

Euchaeta acuta ..... (E) — ⊘

Nannocalanus minor ..... (E) — ▽

WARM - TRANSITIONAL GROUP

Pleuromamma robusta ..... (E) — ◓

Pleuromamma gracilis ..... (E) — ◐

Sagitta serratodentata ..... (E) — ⬓

COLD (NORTHERN)-TRANSITIONAL GROUP

Pareuchaeta norvegica ..... (E) — ◑

WARM - TRANSITIONAL - NERITIC GROUP

Euchaeta hebes ..... (E) — ⊖

Candacia armata ..... (E) — ●

Centropages typicus ..... (T) — ○

Spiratella retroversa ..... (E) — ◆

GENERAL - NERITIC GROUP

Metridia lucens ..... (E) — ⊕

Acartia clausi ..... (T) — ⊗

COASTAL (NERITIC) GROUP

Temora longicornis ..... (T) — X

Sagitta elegans ..... (E) — ◹

Sagitta setosa ..... (E) — ◪

"*Nil*" PLANKTON; STATIONS IN :

Oceanic waters - - - - - - - - - - - - - - - - - - ●

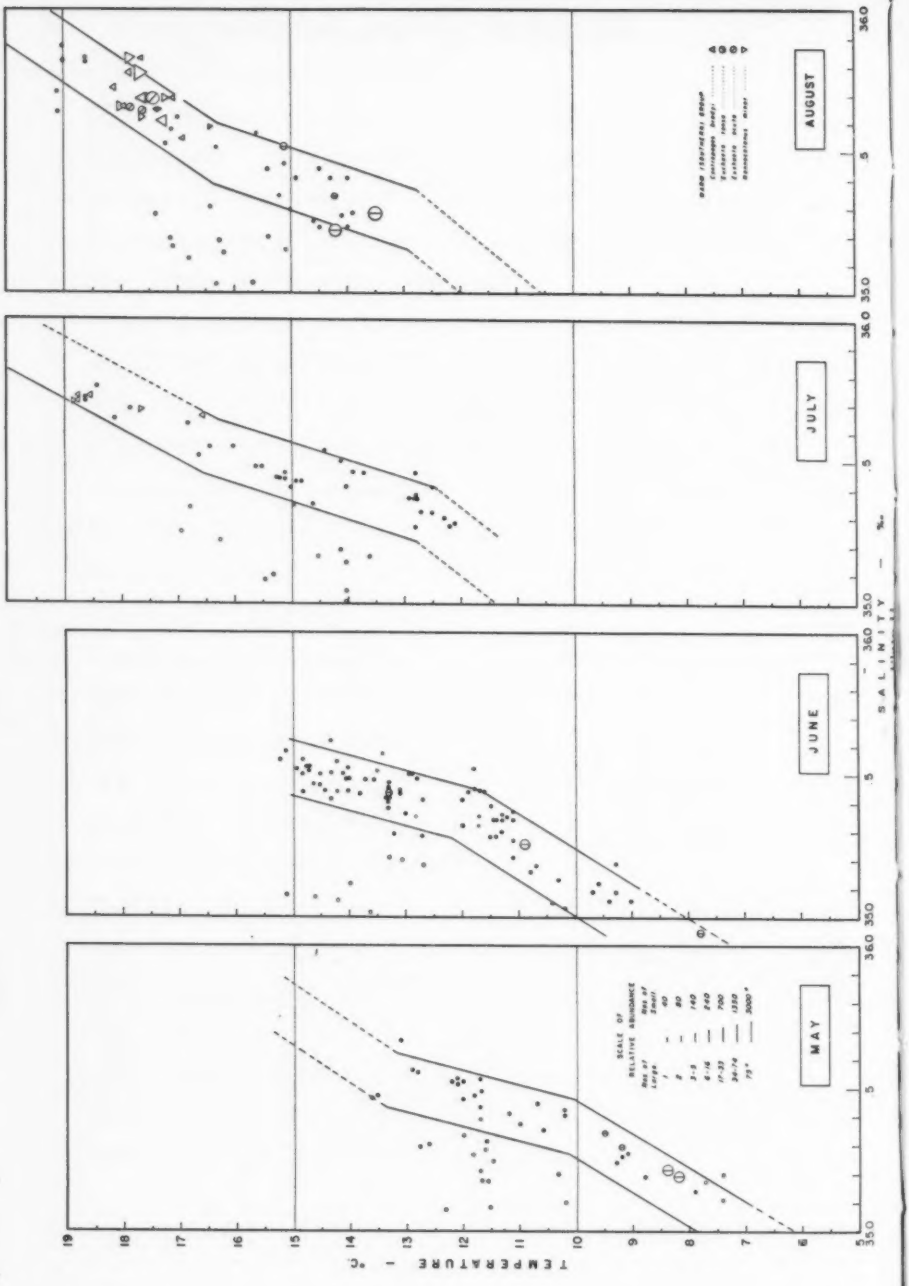
Coastal waters - - - - - - - - - - - - - - - - - - ○

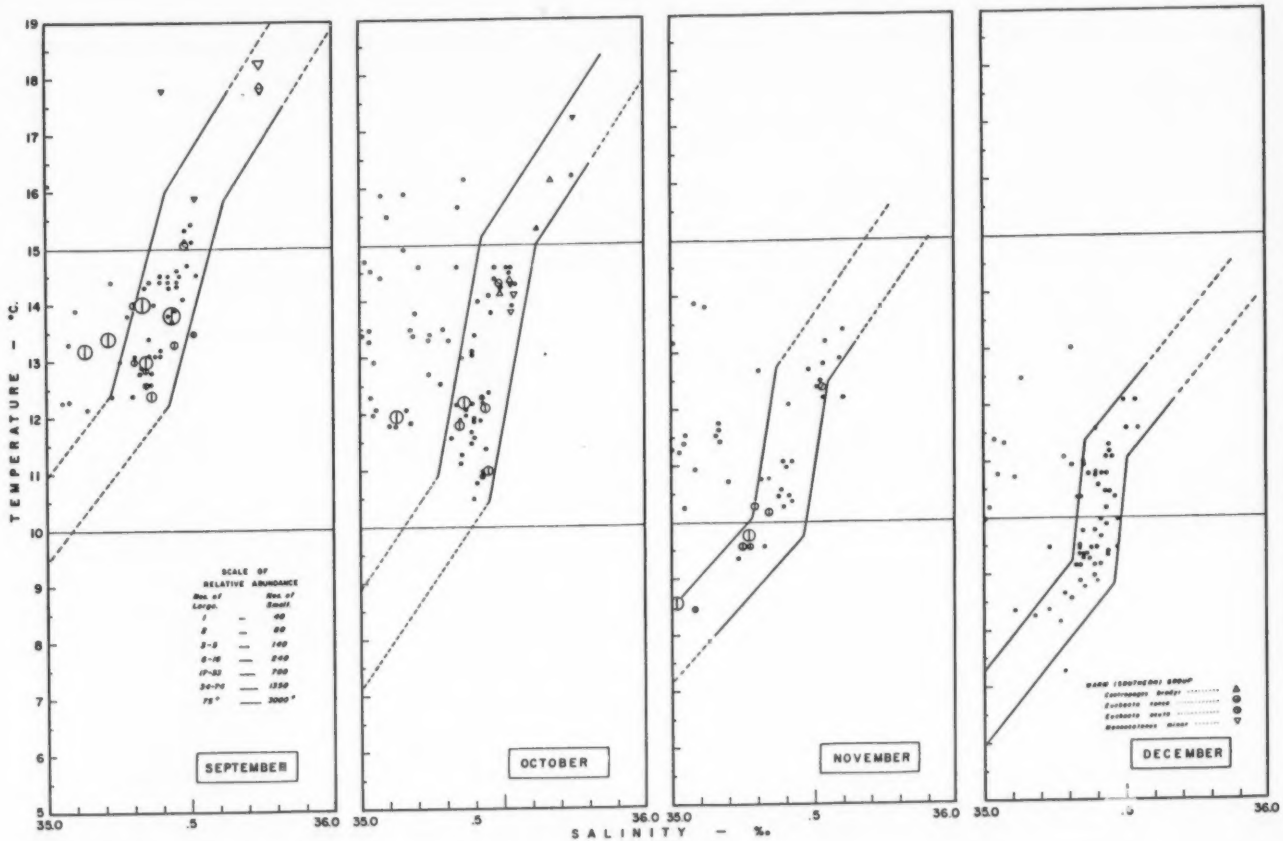
* E = "Eye - count" = Large organisms

T = " Traverse " = Small organisms

JANUARY
FEBRUARY
MARCH
APRIL
SCALE OF RELATIVE ABUNDANCE
SALINITY — ‰
TEMPERATURE — °C

Plate I.


AUGUST
JULY
JUNE
MAY
SALINITY - ‰
TEMPERATURE - °C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SALINITY — ‰
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
SCALE OF RELATIVE ABUNDANCE

Plate III.

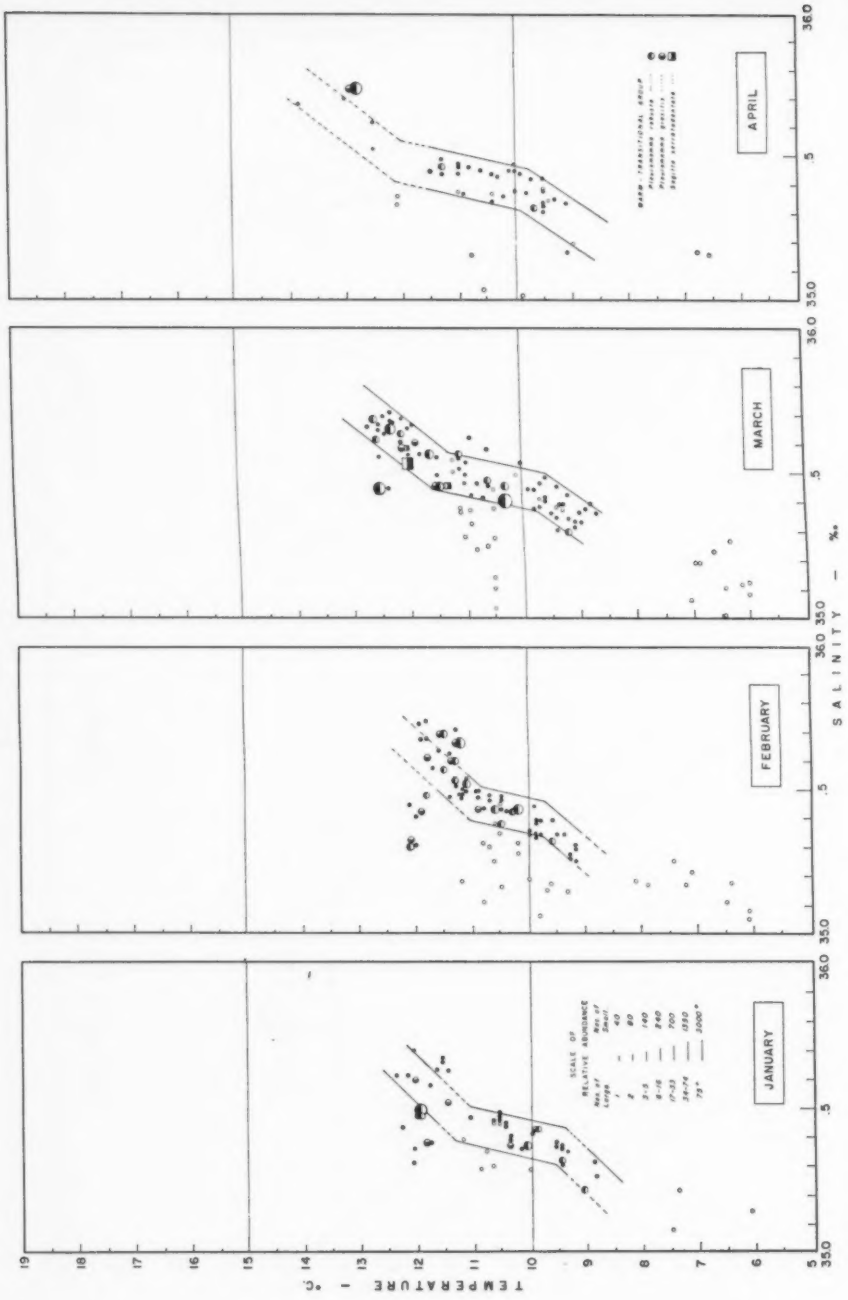

JANUARY
FEBRUARY
MARCH
APRIL
SCALE OF RELATIVE ABUNDANCE
TEMPERATURE - °C.
SALINITY - ‰

Plate IV.

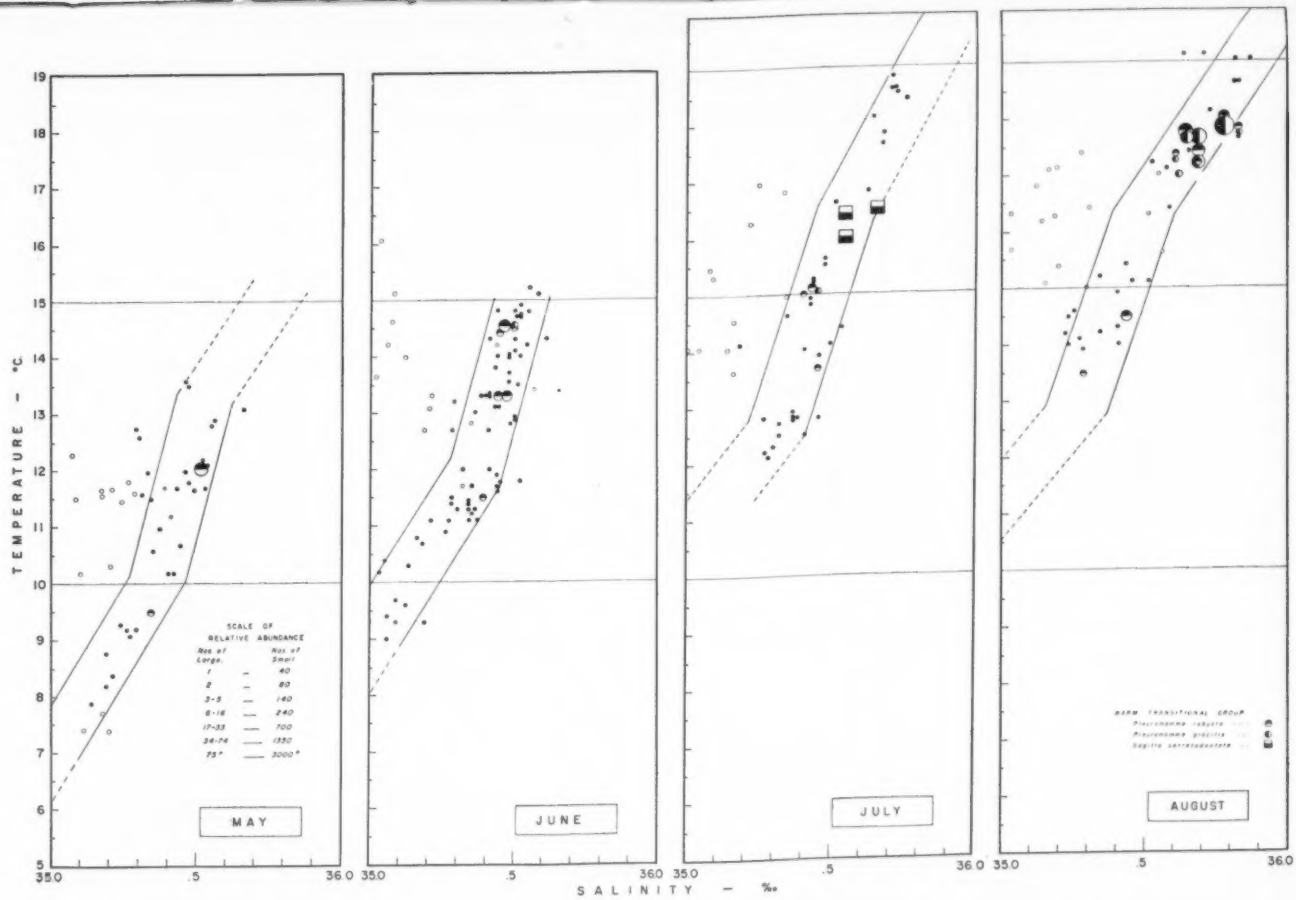

TEMPERATURE — °C.
SALINITY — ‰
MAY
JUNE
JULY
AUGUST
SCALE OF RELATIVE ABUNDANCE
Nos. of Large.
Nos. of Small
1 — 40
2 — 80
3-5 — 140
6-16 — 240
17-33 — 700
34-74 — 1350
75+ — 3000+
WARM TRANSITIONAL GROUP
Pleurobrachia rhodopis
Pleurobrachia globosa
Sagitta serratodentata

Plate V.

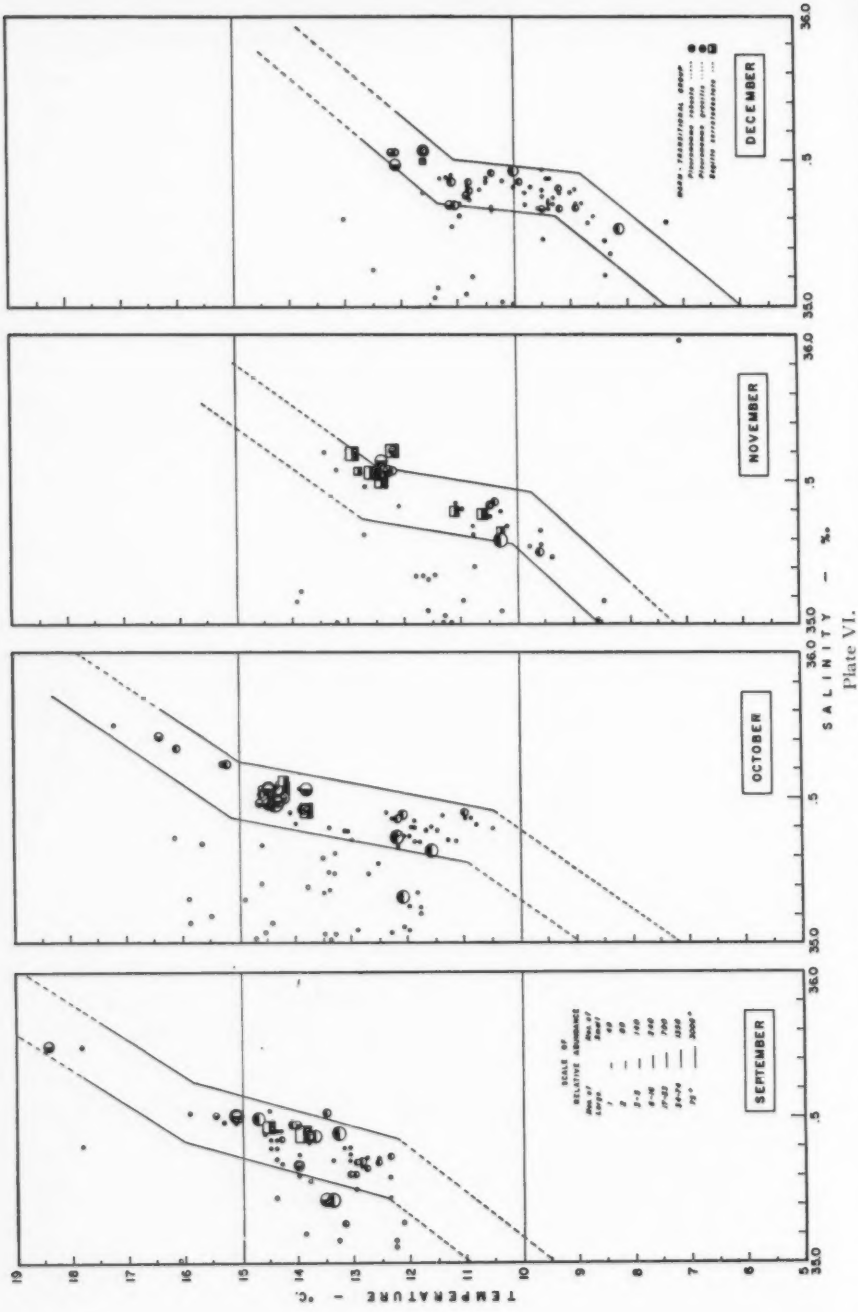

DECEMBER
NOVEMBER
OCTOBER
SEPTEMBER
SALINITY - ‰
TEMPERATURE - °C.

Plate VI.

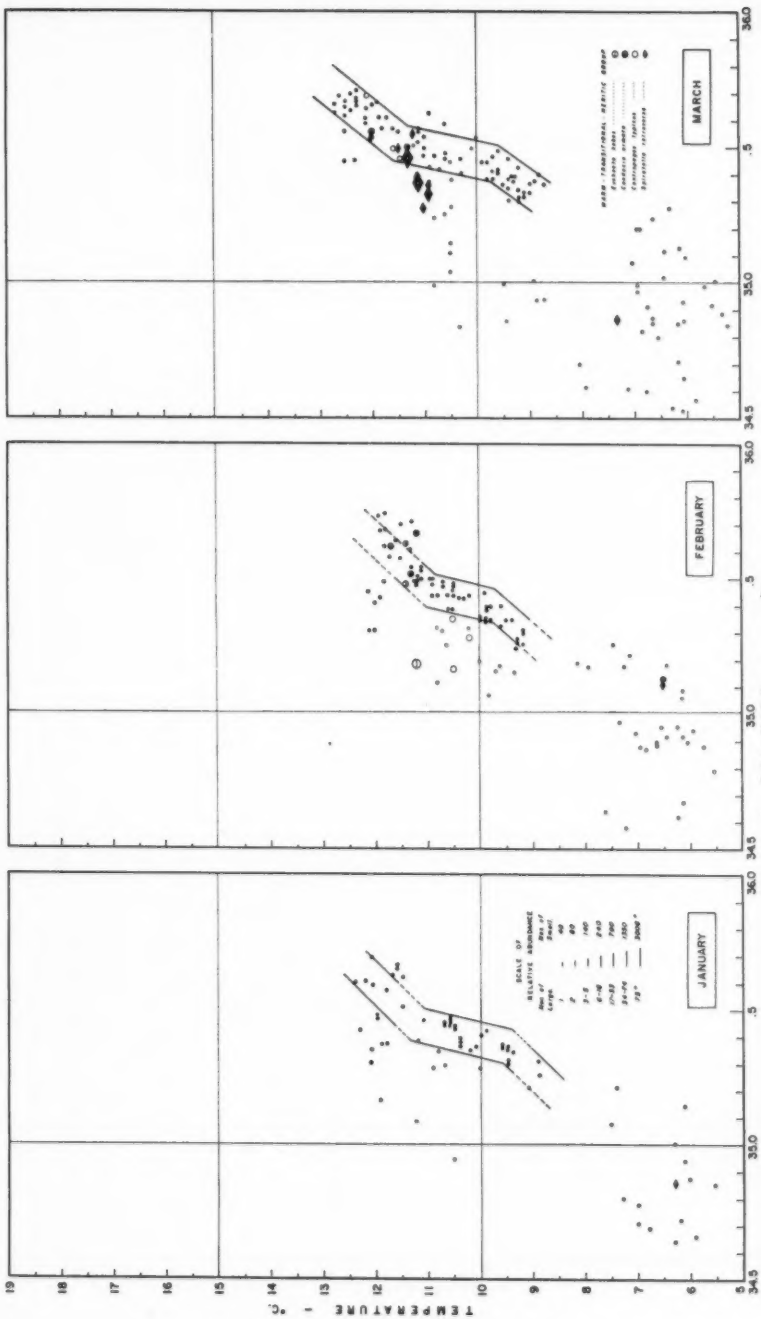


Plate VII.

Plate VI.

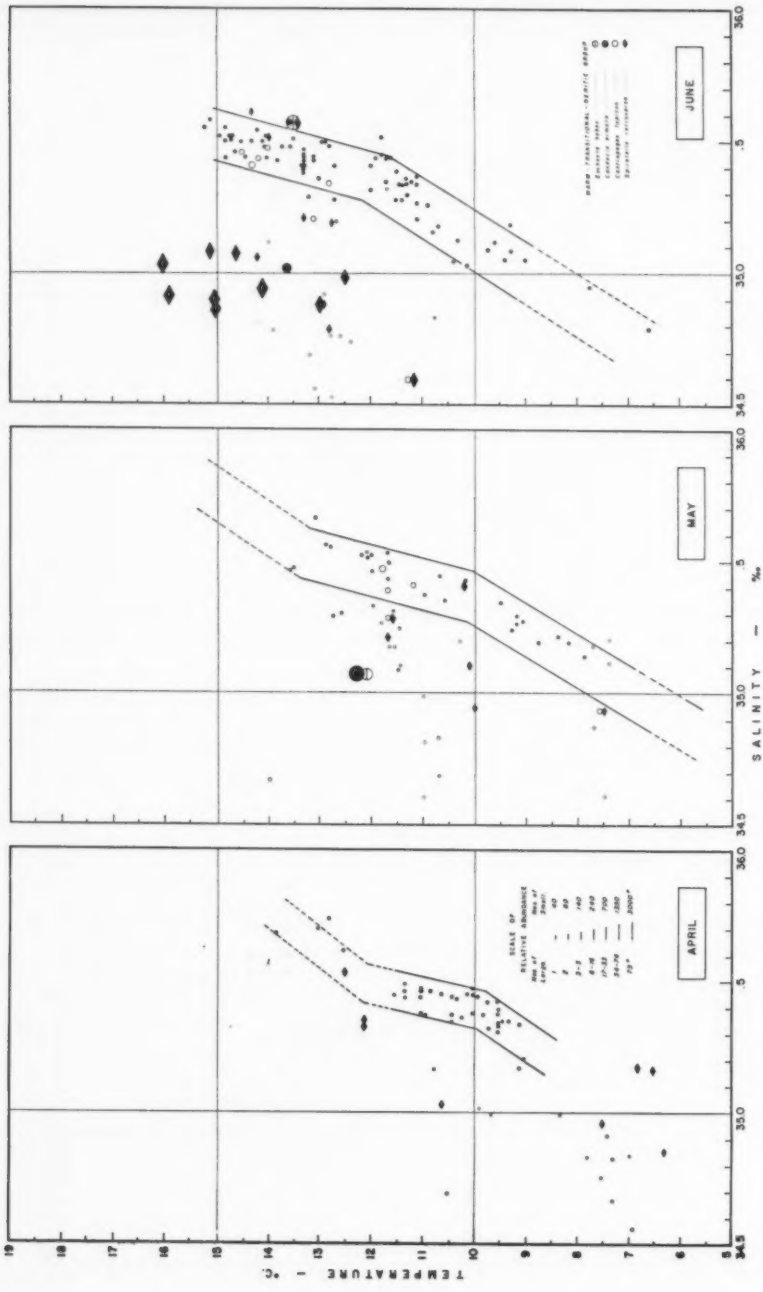
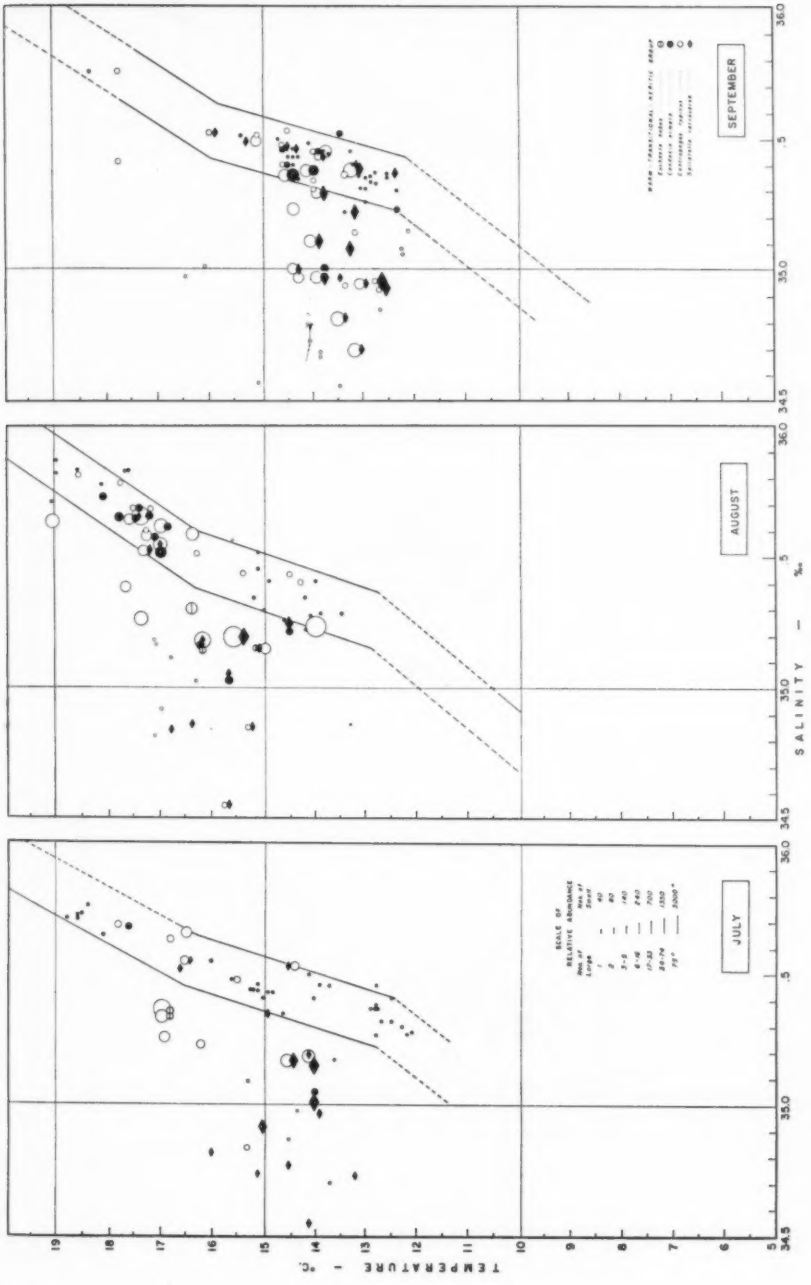


Plate VIII.



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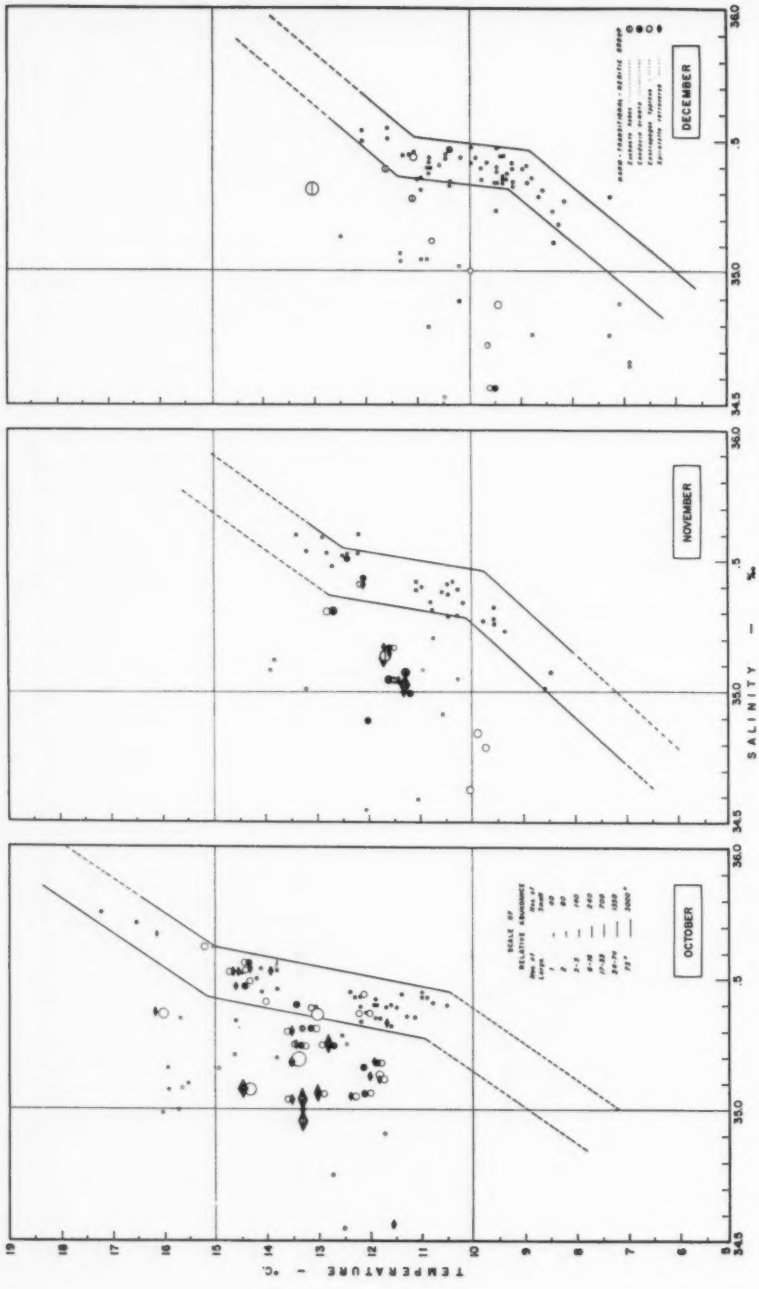

Plate X.

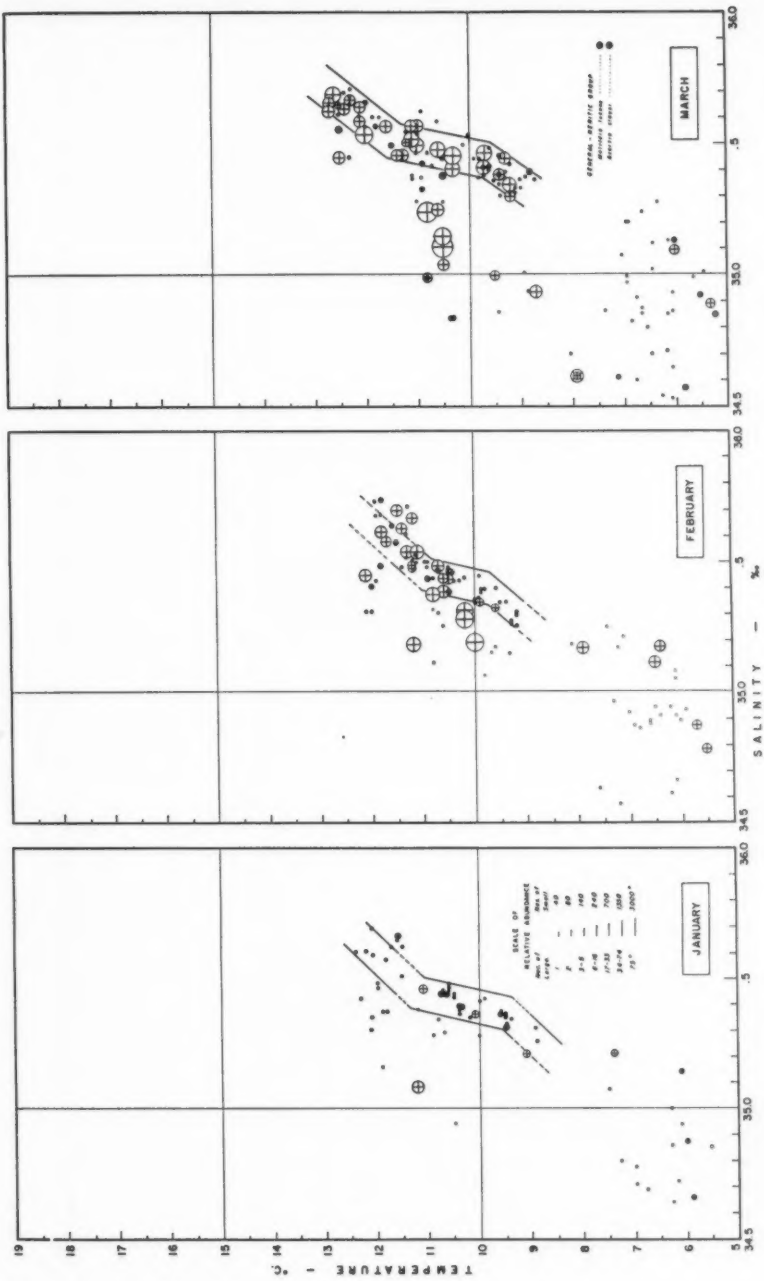

Plate XI.

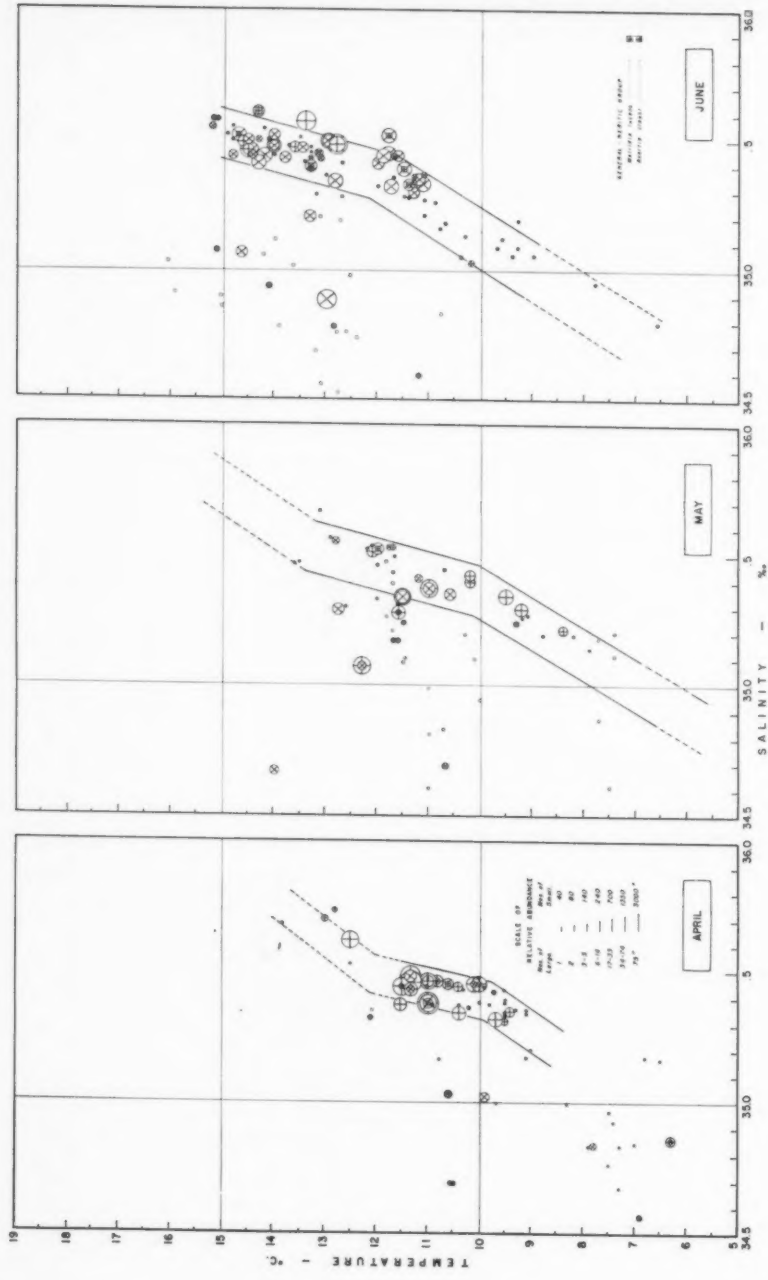

Plate XII.

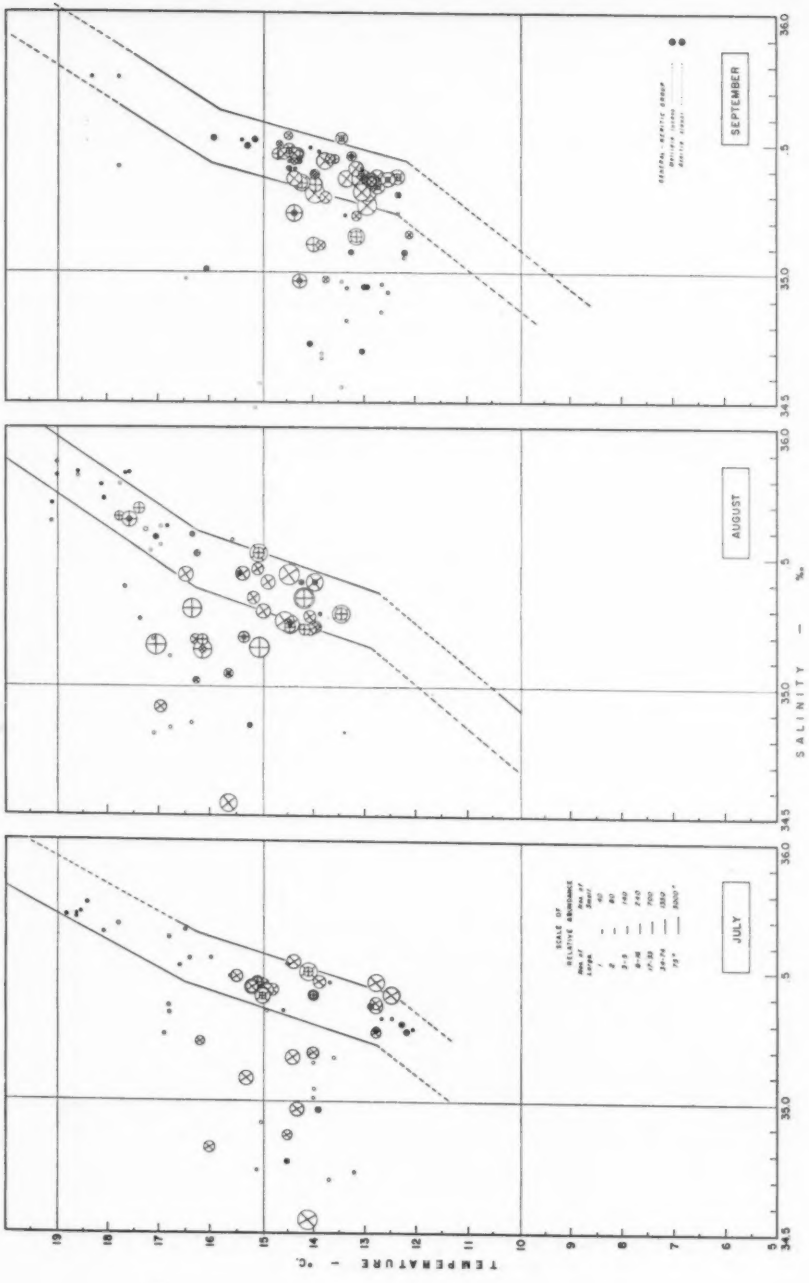
JULY
AUGUST
SEPTEMBER
SCALE OF RELATIVE ABUNDANCE
TEMPERATURE - °C.
SALINITY - ‰

Plate XIII.

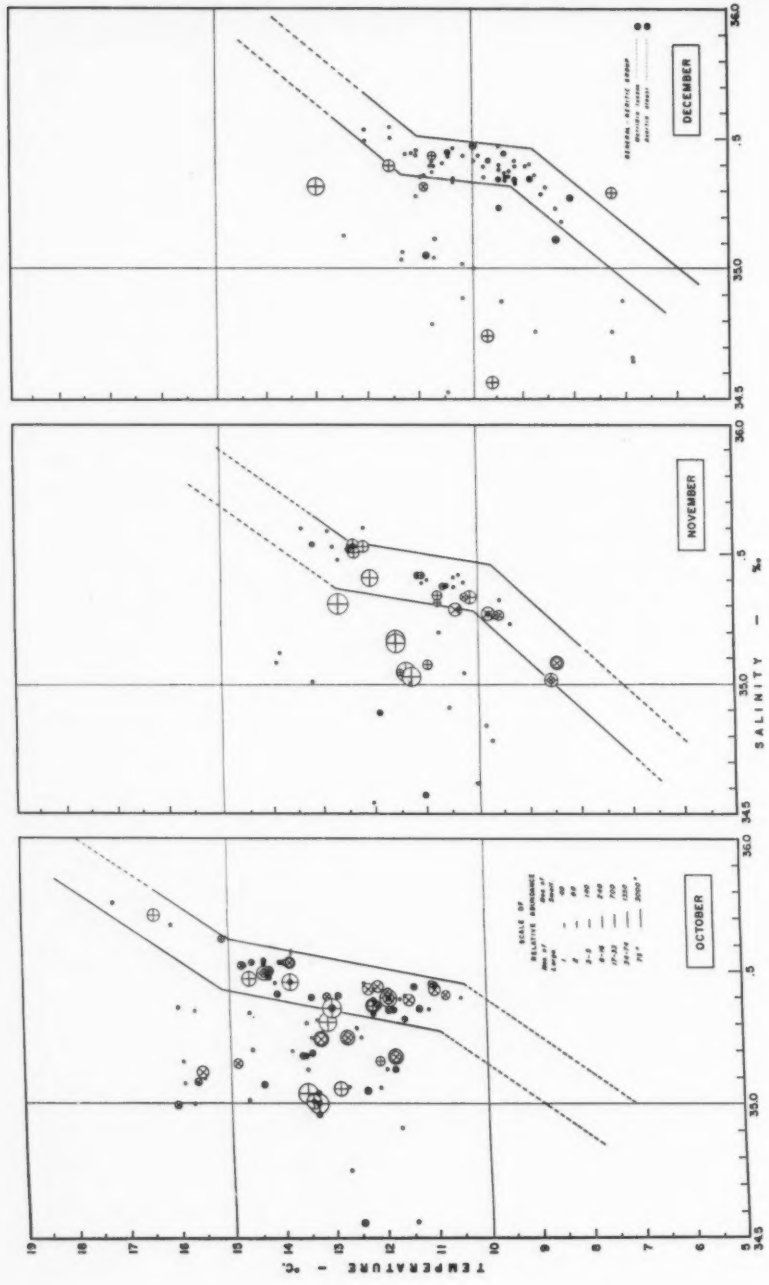

Plate XIV.

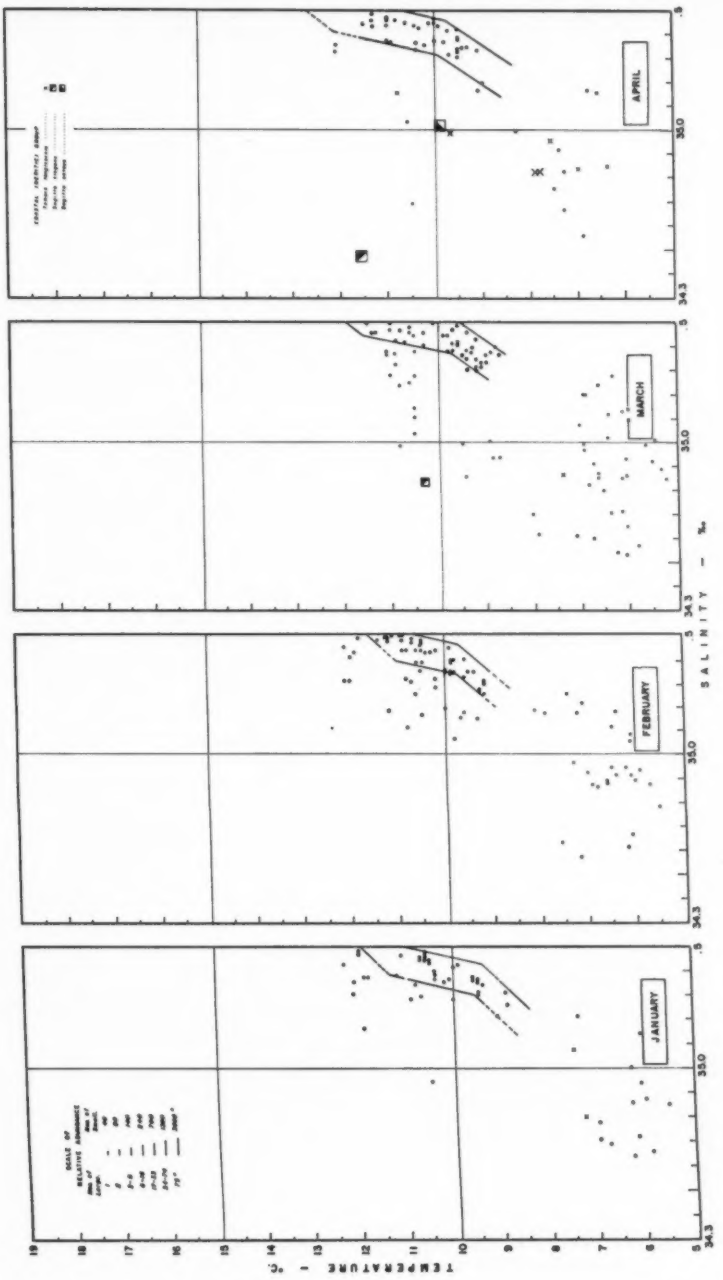

Plate XV.

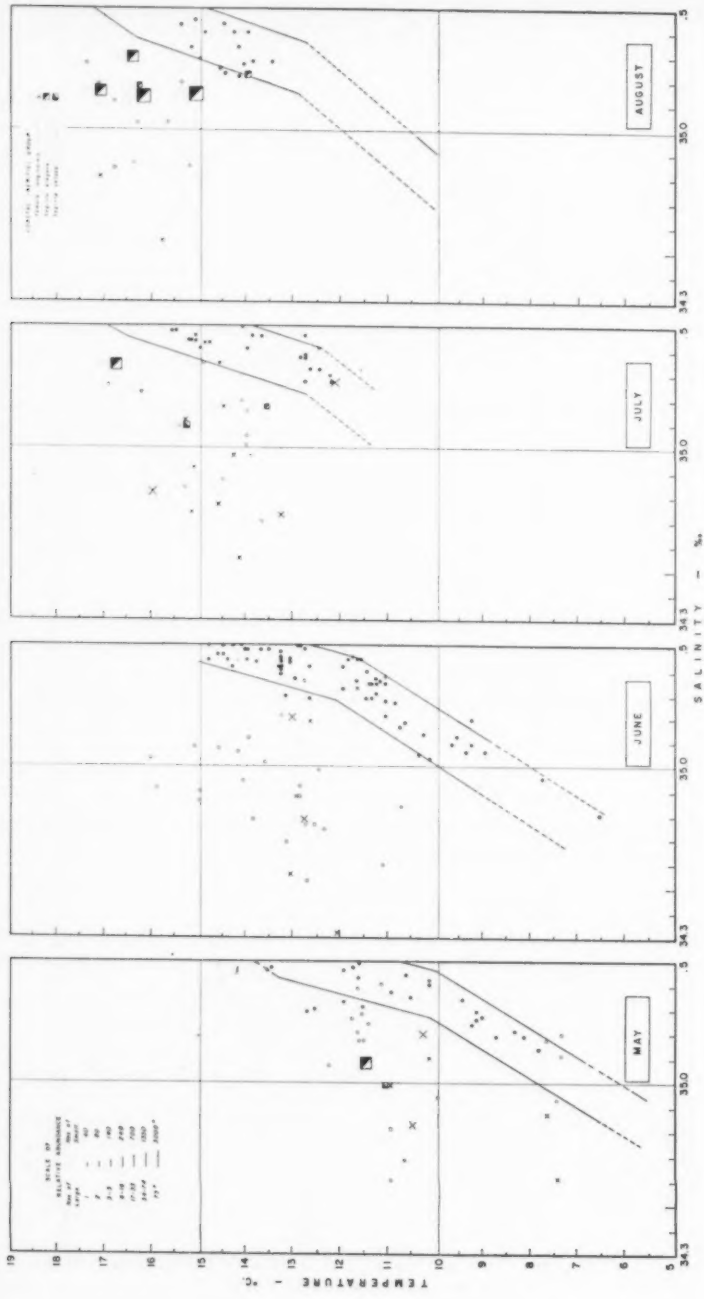

Plate XVI.

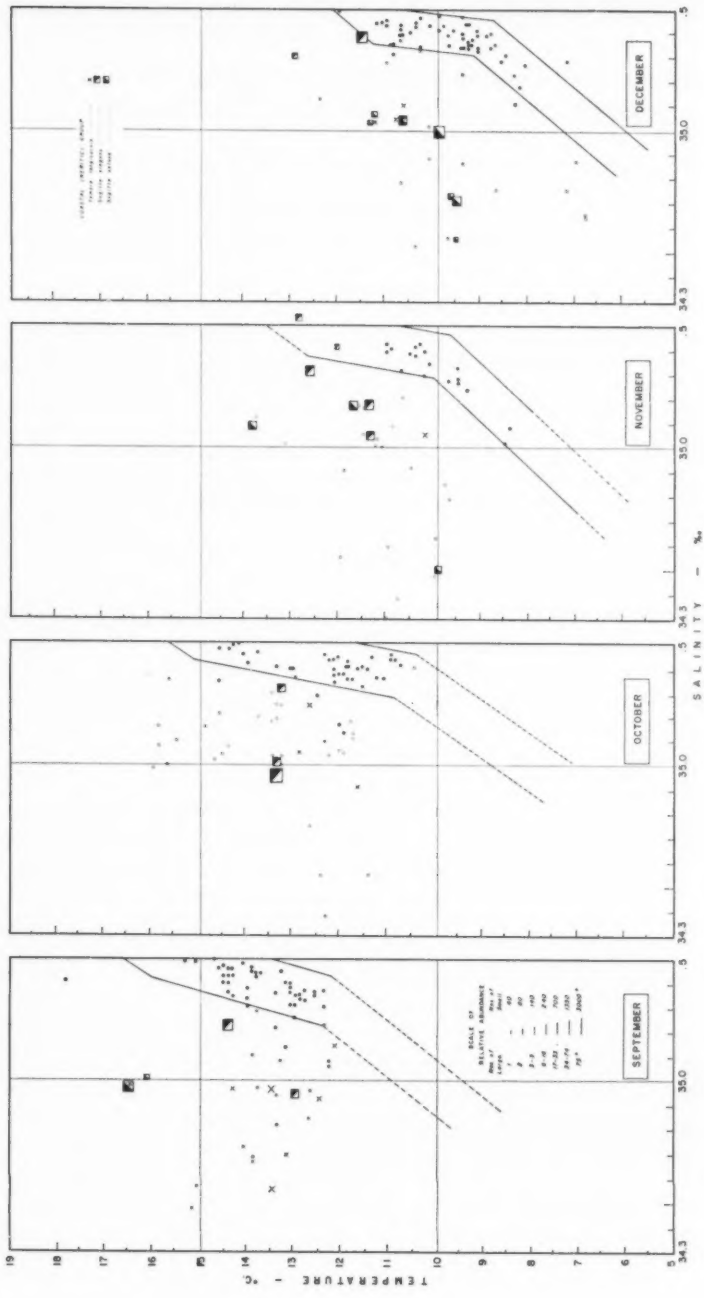
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
TEMPERATURE - °C
SALINITY - ‰

Plate XVII.

An Investigation of Herring (*Clupea harengus* L.) Spawning Using Free-Diving Techniques[1]

By S. N. Tibbo, D. J. Scarratt and P. W. G. McMullon

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Free-diving (Scuba) techniques were used to survey a herring spawning bed near Blanchard Point, Chaleur Bay, N.B., in May 1962. The spawning bed occupied a long, narrow area running parallel with and near the shore in depths of 4–20 feet (1.3–6 m). The total area surveyed was 448,800 square yards (375,200 sq m) and the total number of herring eggs was estimated to be 35.46×10^{11}. The number of spawning herring was calculated to be 185 million fish (54.7 million pounds or 24,812 metric tons). The commercial fishery took 2.2 million pounds (998 metric tons) in the vicinity of the survey area which represents a fishing mortality rate of 4.0%. Hatching started about May 24 when large numbers of herring larvae 5–7 mm long were captured with plankton nets.

INTRODUCTION

The locations of herring spawning areas in the Northwest Atlantic are poorly defined and few attempts have been made to determine the density of eggs on spawning beds or the production of larvae from various spawnings. Earll (1887), Moore (1898), Huntsman (1919), Jean (1956), Tibbo (1956, 1957a, b, c) and Day (1957a, b) have all made reference to the time and location of herring spawnings in parts of the Canadian Atlantic area but McKenzie (personal communication) seems to have been the only investigator in this area to attempt accurate mapping, measuring and sampling of a spawning bed and from this calculating the total egg deposition and the size of the spawning stock.

In other areas, Hart and Tester (1934) reported a quantitative study of herring (*Clupea pallasii*) spawning in Departure and Nanoose Bays on the east coast of Vancouver Island, British Columbia; Runnström (1941) made a similar study of herring (*Clupea harengus*) spawning and its yearly fluctuations on the west coast of Norway; Tester and Stevenson (1948), Stevenson and Outram (1953), Taylor and Outram (1954), Taylor (1955), Taylor *et al.* (1956, 1957), all described the extent and intensity of herring (*Clupea pallasii*) spawnings in British Columbia waters; Skud (1959) described herring (*Clupea pallasii*) spawning in southeastern Alaska. Bolster and Bridger (1957) described the nature of herring (*Clupea harengus*) spawning areas in the English Channel; and Parrish *et al.* (1959) carried out surveys of herring (*Clupea harengus*) spawning and larval distribution in the Firth of Clyde.

The Pacific herring (*Clupea pallasii*) spawns in or just below the intertidal zone and hence no special techniques are involved in observations of spawning

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areas. In contrast, the Atlantic herring (*Clupea harengus*) spawns below the intertidal zone in depths varying from 2 to 3 fathoms (4 to 7 m) down to 100 fathoms (180 m), and in the studies on this species observations were made with bottom grabs of various kinds, although Parrish *et al.* (1959) used, in addition, an underwater camera to photograph parts of the spawning beds.

In the investigation reported here, the principal technique was free diving although a Petersen grab was used both at the beginning and near the end of the survey. The free-diving technique was better for outlining the spawning beds, describing their nature and in obtaining representative samples of herring eggs.

The present study was conceived by the senior author who was responsible for mapping the area and processing egg samples. Both junior authors participated in the free diving and were responsible for the descriptions of the techniques adopted underwater, the description of the physical appearance of the bed, and for the photographs.

GENERAL OBSERVATIONS ON HERRING SPAWNING

Bigelow and Schroeder (1953) described herring spawning in the Northwest Atlantic as follows:

"Herring may spawn in spring, in summer or autumn, according to locality, or both in spring and autumn. They do so chiefly on rocky, pebbly, or gravelly bottoms, on clay to some extent, probably never on soft mud. Spawning in the Gulf of Maine (including the Bay of Fundy), takes place chiefly from 2 or 3 fathoms down to about 30 fathoms; perhaps never in the littoral zone, nor has herring spawn ever been reported as cast up by the surf on the beaches of New England, a fate that often overtakes it in the Gulf of St. Lawrence. Occasionally they spawn as deep as 100 fathoms in Scandinavian waters, perhaps also in the eastern basin of our Gulf where the sea floor is hard, not soft and muddy as it is in the basins in the western side. During the act of reproduction as observed by Moore at Cross Island and at Machias, Maine, 'the fish were darting rapidly about, and those who have opportunity to see the fish spawning in more shallow water where observation is more favorable, state that both males and females are in constant motion, rubbing against one another and upon the bottom, apparently by pressure aiding in the discharge of the eggs and milt'.

"A female herring may deposit from 20,000 to upwards of 40,000 eggs, according to her age and size, averaging about 30,000. In sexually mature herrings, the genital organs are so large just before spawning commences that they make up about one-fifth the total weight of the fish.

"The eggs sink to the bottom, where they stick in layers or clumps to the sand or clay, to seaweeds, or to stones, by means of their coating of mucus, or to any other objects on which they chance to settle. They are often found massed on net warps, anchors, and anchor ropes. The individual eggs are 1 to 1.4 mm in diameter, depending on the size of the parent fish and also, perhaps on the local race of fish involved . . ."

This description, while basically correct, is so general that it contributes little to an understanding of herring spawning in specific areas and seasons.

In the Chaleur Bay area of the Gulf of St. Lawrence there are two spawning seasons (spring and autumn) for herring but no attempt has been made previously to describe the spawning beds or to estimate the size of the spawning stocks. Jean (1956) and Tibbo (1957a) both described population characteristics of the spring- and autumn-spawning stocks in Chaleur Bay but made only general reference to spawning areas and seasons.

Perley (1852) gave approximate times of appearance and disappearance of spring- and autumn-spawning herring in the Gulf of St. Lawrence. These were from late April or early May to about June 10 for spring spawners and from about August 20 to about September 20 for autumn spawners. These dates still apply and the only additional evidence of spawning available until now has been assumed from study of the commercial fishery. The locations of the better catches suggest that spawning takes place in very shallow water (2–3 fm or 4–6 m) in the spring but considerably deeper (10–12 fm or 18–22 m) in the autumn.

SURVEY OF A HERRING SPAWNING BED

Herring spawning was studied throughout the period May 15–24, 1962. It was evident that herring were spawning in the Caraquet area on May 14 because all the fish that were landed by commercial fishermen were in the "ripe and running" stage. Fishermen stated that the herring had been in this condition for at least a week or ten days. Reports by fishermen and Fisheries Officers indicated that there were at least four major spawnings taking place over a distance of 10 nautical miles (18.5 km) eastward of Caraquet, N.B., in Chaleur Bay. The site chosen for observation was in the vicinity of Blanchard Point (Fig. 1), where most of the commercial fishing activity was centered in mid May. In the Blanchard Point area heavy deposits of herring eggs were observed on fishing nets especially on a herring trap. The leader and walls of this trap were encrusted with herring eggs and there was a heavy deposition on the bottom

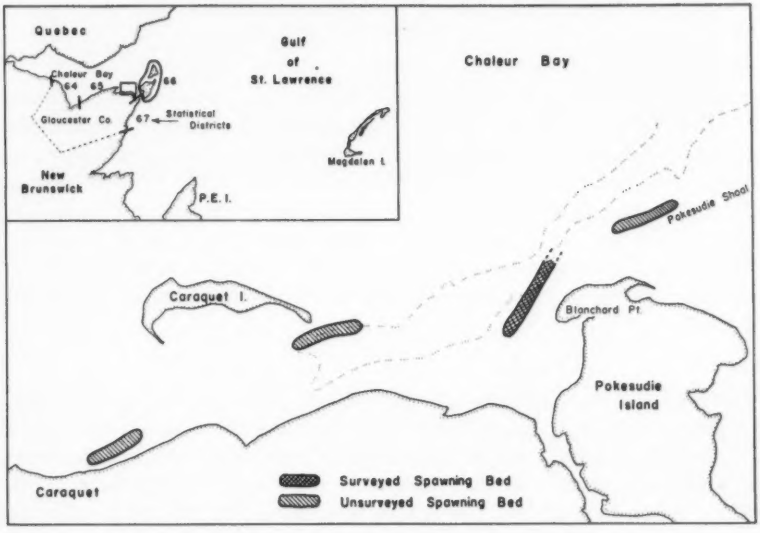

FIG. 1. Chart of the southeast portion of Chaleur Bay showing spawning areas and places referred to in the report. Gloucester County and statistical district boundaries shown in inset.

and on the eastern (or downstream for non-tidal drift) side of the trap. Patches of "white" water in the area gave additional evidence of spawning.

Petersen Grab

A preliminary examination of the Blanchard Point spawning area was made on May 15 with a Petersen grab whose dimensions were $9\frac{1}{2} \times 10\frac{1}{2}$ inches (24 × 27 cm). Many of the grab samples contained large masses of herring eggs and indicated that the spawning area was a long, narrow bed parallel to the shore in depths of 6–20 feet (2–6 m). The long axis of this bed was in line with the main direction of the tidal movement.

In general the Petersen grab samples indicated that herring eggs were deposited two or three eggs thick on seaweeds (chiefly *Laminaria* and *Phyllophora*) although in the vicinity of the herring trap, spawn appeared to be deposited on the floor of the sea in masses ten to twenty eggs thick.

The Petersen grab samples indicated an extreme patchiness in the deposition of eggs since more than half of the attempts to obtain samples gave negative results. This was noticeably the case where the bottom was covered with large stones 4–8 inches (10–20 cm) in diameter. These stones apparently caught in the jaws of the grab on the bottom and then slipped out taking with them the seaweed and any attached eggs on their way to the surface. In fact, in many locations where heavy deposits of herring eggs were discovered later, none were taken with the Petersen grab. Similarly, the grab did not sample egg-encrusted seaweed efficiently. Frequently it contained only small torn pieces of seaweed with attached eggs indicating a very light spawning whereas actually it was quite heavy.

Scuba Diving

Direct observations of the Blanchard Point spawning bed were made on May 18, 19, 21 and 22 by two divers using self-contained underwater breathing apparatus (Scuba). Expanded neoprene "wet"-type diving suits were worn and dives of up to an hour duration were made with comfort. The surface-water temperature varied from 5.4 to 6.3°C. Dives were made from lifeboats 18 feet (5.5 m) long usually with one diver to a boat, one or two men at the oars and another man as diver's attendant and recorder. The two divers worked independently except during the initial exploratory dives and when photographs were being taken.

Mapping

For mapping the spawning area both divers swam together toward the bed from a point outside it. When herring eggs were first encountered on the bottom both divers surfaced and a small buoy complete with weight and line was dropped in the water near them. These buoys were made out of polystyrene net floats 4 inches (10 cm) in diameter. A groove was cut in the edge of the disc and a length of light nylon line (9-thread medium seine twine) tied to the float wound around the groove in the manner of a "yo-yo". A 4-ounce (113-g) lead weight was tied to the free end of the line and the whole was kept together with an elastic

FIG. 2. Underwater photograph showing a sample of herring eggs being taken with a "cookie cutter".

band. The buoys could be released easily by a diver on the bottom merely by removing the rubber band and thus releasing the float, although in shallow water it was quicker for the diver to surface and have the buoy dropped from the boat. When both divers were satisfied that the first buoy was accurately placed on the outer edge of the bed they continued to follow the edge of the bed, one eastward and the other westward.

In contrast to spawning observations made in the Firth of Clyde in 1958 (Parrish *et al.*, 1959) the edge of the spawning bed at Blanchard Point was nowhere a discrete line. Rather the eggs gradually became less dense until none could be seen. The divers' paths tended to follow a zig-zag pattern back and forth across the boundary which could be plotted to within a couple of feet. Each diver surfaced every few minutes and a small buoy was dropped alongside him thus marking the edge of the bed at that point.

When a length of boundary had been explored and marked out in the above manner, the shape and dimensions of the bed were plotted by taking compass bearings between each of the "yo-yos" floating on the surface and establishing their distance apart by means of a range finder. In a series of 4 dives almost 1500 yards (1370 m) of boundary were outlined. The accuracy of the mapping was checked by reference to fixed land marks and navigation buoys and indicated a final error of 10 degrees in direction and 35 yards (32 m) in extent for the total area surveyed.

Sampling

To establish the distribution and density of eggs on the spawning bed a series of transects was made. A boat was first rowed across the area and "yo-yo" buoys dropped at irregular intervals. Later a diver swam back along the line of buoys and sampled the area close by each buoy weight. Standardization of samples was effected by using a form of "cookie cutter" made from 6-inch (15-cm) stovepipe and fitted with a handle (Fig. 2). Because the sea bottom was chiefly stones and sand it was not possible to cut a clean sample of vegetation and herring eggs. It was even more difficult to obtain representative samples on the reef of red sandstone that occupied much of the eastern part of the area surveyed. The usual procedure was to clear the area of all vegetation around the "cookie cutter" as it was held over the sample and then to gather the isolated sample by hand and place it in a polythene bag which was immediately brought to the surface and placed in the boat. Samples were not taken at all transect stations, in which cases the diver merely reported the nature of the bottom and egg density (heavy, medium, intermediate, light and very light) to the recorder in the boat. The positions of the transect stations were plotted in the same manner as the bed boundary. Both the boundary lines and sampling stations are shown in Fig. 3. The total number of samples taken was 34 (Table I).

Photography

Underwater photographs of the spawning bed were taken to show sampling and survey techniques and variations in density of egg deposits (Fig. 2, 4, 7).

The equipment used consisted of a Rolleiflex f3.5 camera in a Rolleimarine IV underwater case. The film used was Kodak Plus X Panchromatic. The best results were obtained with 1/30 seconds exposure at f5.6. The "cloudy" appearance of the prints (Fig. 2, 4, 7) is a result of the turbidity of the water rather than the exposure. The photographs were taken without artificial light during the early afternoon in 2–3 fathoms (4–6 m) depth.

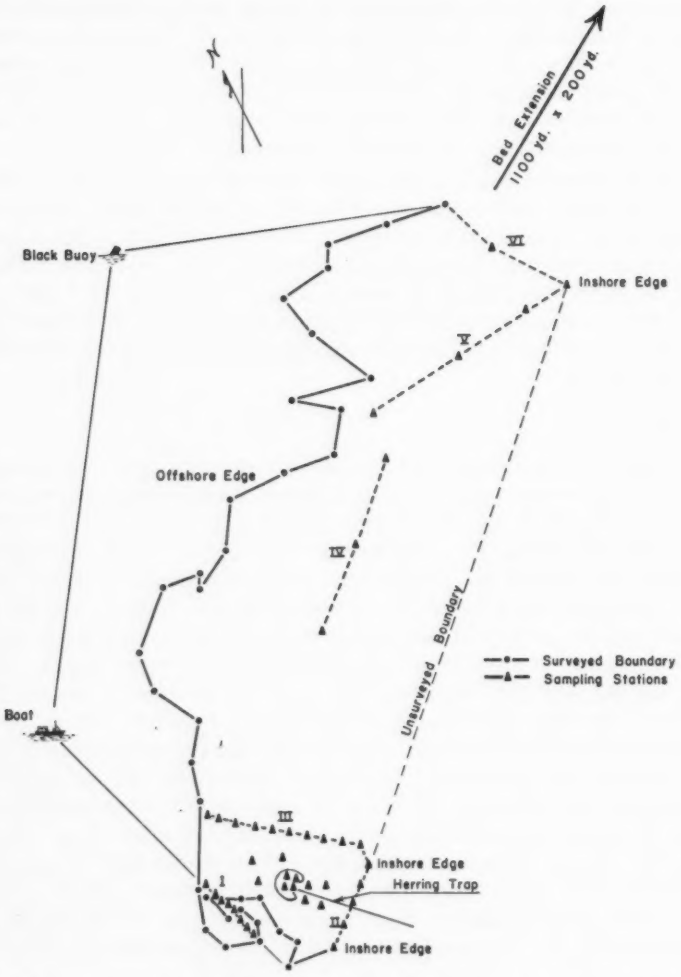

FIG. 3. Drawing of the surveyed area showing spawning bed boundaries, sampling lines and stations (see text for dimensions).

TABLE I. Herring spawning intensity as determined from average egg counts in samples each covering 28.5 square inches of a spawning bed at Blanchard Point, New Brunswick.

Type of egg deposition	No. of samples	Egg density (av. no./sample)
Very light	8	26,035
Light	4	111,050
Intermediate	4	166,748
Medium	12	189,982
Heavy	6	385,712
Total:	34	879,527
Average:	..	173,927

RESULTS OF SPAWNING SURVEY

EXTENT OF SPAWNING AREA

The area of the spawning bed at Blanchard Point was calculated from the boundaries that were established by free-diving techniques and from sampling with a Petersen grab (Fig. 3).

The length of the area surveyed by divers measured 880 yards (805 m). The average width was calculated to be 260 yards (238 m). The area surveyed by divers was therefore 228,800 square yards (191,300 sq m).

Additional surveying was carried out on May 23 with a Petersen grab when divers were not available. This survey extended the known spawning area in an easterly direction for at least 1100 yards (1000 m). The width of this extension was estimated to be 200 yards (180 m) and the area calculated to be 220,000 square yards (183,900 sq m).

Thus, the spawning area surveyed by both free-diving and Petersen grab techniques was 448,800 square yards (375,200 sq m). However, it should be noted that the eastern end of the bed was not clearly defined. In fact, the Blanchard Point spawning bed may have been contiguous with another spawning bed on Pokesudie Shoal (Fig. 1) where most of the fishing activity was centered during the fourth week of May.

BOTTOM TOPOGRAPHY AND VEGETATION

The depth of water on the north (offshore) side of the spawning bed at Blanchard Point was between 15 and 20 feet (5 and 6 m) and the bed shoaled gradually to between 6 and 4 feet (2 and 1 m) in the southwest corner.

The floor of the sea in the part (western) of the bed surveyed by Scuba divers was mainly of small stones and gravel with large masses of red sandstone. Very little information is available for the eastern part of the area but Petersen grab samples indicated a similar type of bottom there with perhaps an even greater proportion of red sandstone outcropping.

In the deeper regions of the spawning area, vegetation consisted mainly of *Phyllophora membranifolia* and *Laminaria saccharina* with occasional patches

of *Furcellaria fastigiata*. It was quite noticeable that the density of eggs upon the algae was reduced where the alga cover was less dense and no eggs were found on bare gravel, sand or rocks (Fig. 4). This observation is in striking contrast to the observations of Parrish *et al.* (1959) who made no reference whatsoever to vegetation but described herring eggs in the Firth of Clyde lying directly on the sea floor in an area of small stones and gravel. It is also in contrast to the results of preliminary surveys in the Blanchard Point area when samples taken with a Petersen grab suggested some spawning directly on the floor of the sea. However, this could have resulted from the Petersen grab taking a sample of eggs without disturbing the underlying vegetation.

In the shallower areas of the spawning bed at Blanchard Point the vegetation became mainly of *Chondrus crispus*, *Fucus evanescens* and *Ascophyllum nodosum*. Beyond the bed on the southwest (inshore) side was an area of *Zostera marina* but the eggs did not extend much onto this vegetation. This is in contrast to the observations of Hart and Tester (1934) who reported Pacific herring spawning chiefly on "eel grass" (*Zostera*) or rockweed (*Fucus*). Figures 5 and 6 illustrate the different types of vegetation and the variations in egg deposits at the Blanchard Point spawning area.

Distribution and Density of Eggs

Inside the herring trap at Blanchard Point egg density was very high and the bottom had the appearance of a snow bank. This region of high egg density extended southwards along the line of the trap leader and it was noticeable that it extended farther on the east side of the leader than it did on the west. At the point where transect No. II (Fig. 3) crossed the leader there was an abrupt change from heavy to light density and this pattern persisted to within a few yards of the trap entrance where the density on the western side increased.

In the eastern part of the spawning bed the pattern of egg deposition was essentially the same as in the western part although there were much heavier deposits of spawn in the deeper areas. Here, again, there were no eggs deposited anywhere except on vegetation (there were no fishing nets in that part of the area) and the density of the egg deposits was clearly related to the abundance of seaweeds.

Abundance of Eggs and Number of Spawners

The number of eggs on the spawning bed at Blanchard Point was calculated from samples that were taken with the "cookie cutter" in areas that were described by Scuba divers. For descriptive purposes the density of egg deposition (including compensation for bare areas) was divided roughly into 5 categories and described as very light, light, intermediate, medium and heavy. The actual egg counts corresponding to these descriptions varied from 26,035 for very light depositions to 385,714 for heavy depositions (Table I). The area of the sea floor from which each sample was taken was 28.5 square inches (183.9 sq cm).

The average number of eggs per 28.5 square inches (183.9 sq cm) for the whole spawning bed (Table I) was arrived at from the number of samples in the

FIG. 4. Underwater photograph showing herring eggs on seaweeds—none on bare ground.

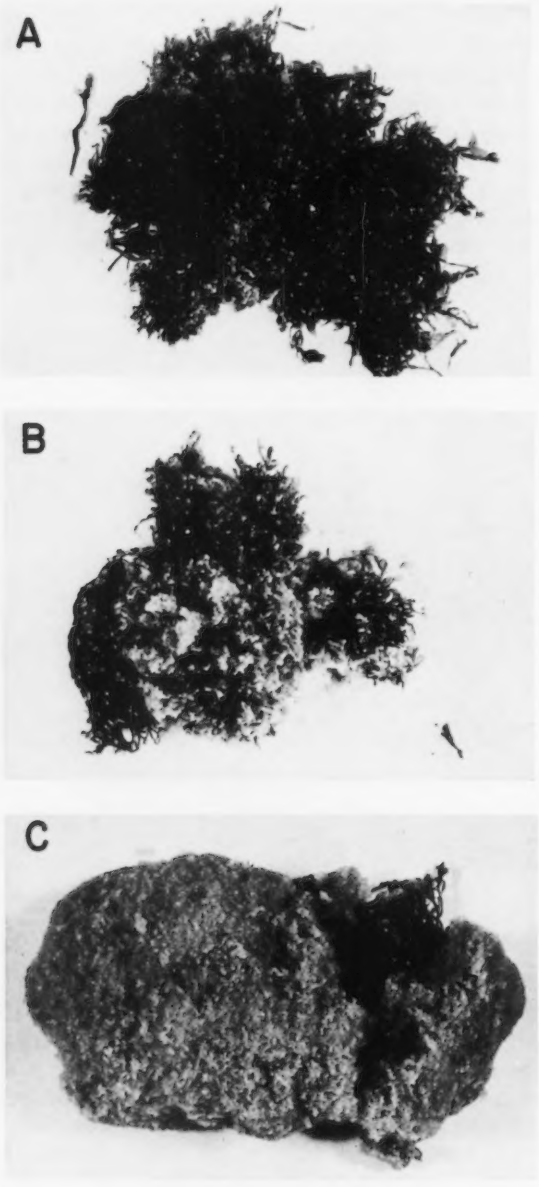

FIG. 5. Photographs showing herring eggs in various density-descriptive categories. (A) light, (B) medium, (C) heavy. Seaweed is chiefly *Phyllophora* sp.

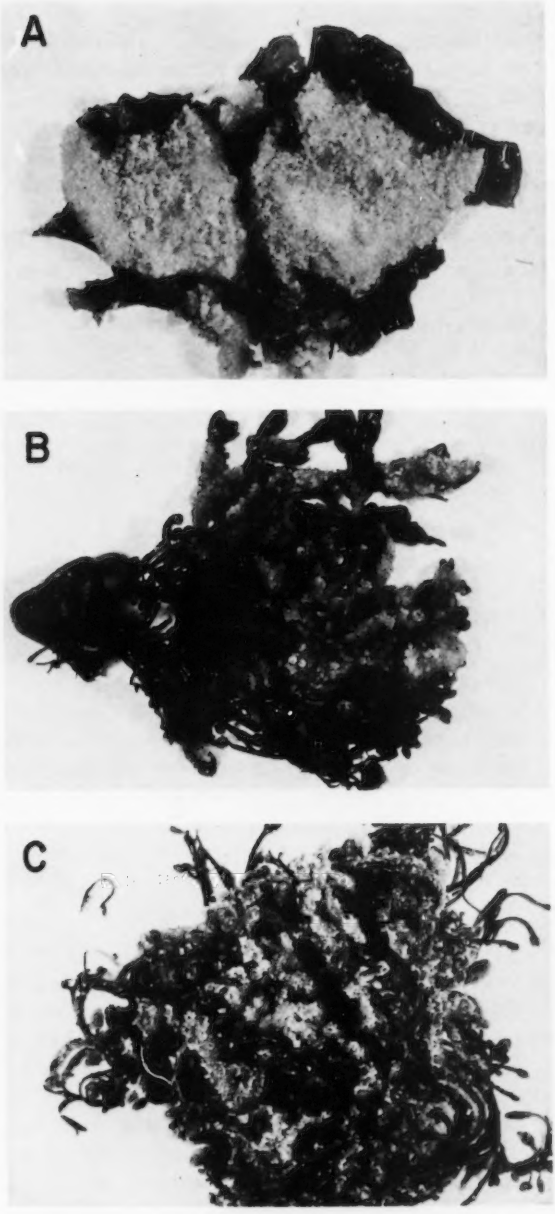

FIG. 6. Photographs showing herring eggs on various types of vegetation. (A) *Laminaria*, (B) *Fucus*, (C) *Ascophyllum*.

various density-descriptive categories multiplied by the number of eggs in the various samples. This was in effect a contouring of the whole spawning bed from which an average egg deposition was calculated.

Estimates of the total number of eggs on the spawning bed and the herring population responsible for it are given in Table II. The fecundity figures are from prespawning herring taken at Magdalen Islands in 1962 rather than in Chaleur Bay. All of the herring taken in Chaleur Bay were in the "ripe and running" condition and because of this no reliable estimate of fecundity was obtainable. However, fecundity figures for Magdalen Islands herring can be

TABLE II. Estimation of the numbers of herring eggs and spawners on the Blanchard Point spawning bed, based on fecundity of herring = 3.85×10^4, and sex ratio = 50:50.

Description of egg deposition	Portion of bed covered	Av. no. of eggs/sq yd	Size of spawning area in sq yd	No. of eggs	No. of spawners (♂ + ♀)
	%	$\times 10^0$	$\times 10^6$	$\times 10^{11}$	$\times 10^6$
Very light	23.5	1.18	1.06	1.25	6
Light	11.8	5.05	0.53	2.68	14
Intermediate	11.8	7.58	0.53	4.02	22
Medium	35.3	8.64	1.58	13.65	71
Heavy	17.6	17.54	0.79	13.86	72
Total:	100.0	...	4.49	35.46	185
Average:	...	7.91	...	...	...

used with reasonable confidence since they are located in the same general area of the Gulf of St. Lawrence and are of approximately the same size. For the purpose of calculation the sex ratio was assumed to be 50:50, although in 5 samples (500 fish) examined for size, age, sex and maturity, the actual ratio of males to females was 51:49. The spawning population of herring on the Blanchard Point spawning bed was estimated at 185 million fish (Table II). This figure is undoubtedly low because the total spawning area was not covered.

FISHING MORTALITY

A comparison of the estimated size of the spawning stock with commercial catches of herring taken during the spawning season provides information on the rate of exploitation. The fishery in 1962 started in late April and extended into the early part of June. About 90% of the total landings were made in May. Fishing was mainly with anchored gill nets although two and possibly more traps were used. The anchored gill nets varied in mesh size from 2 to 2½ inches (5.0 to 6.5 cm) stretched measure. They were set across the current and, weather permitting, were hauled every morning. One trap that was set close inshore (maximum depth in the pocket 20 feet or 6 m) was observed carefully over a 4-day period. This trap fished continuously and the fish were removed by a "spiller" whenever markets and transportation facilities were available.

The proportion of the total spawning stock taken by the fishery was calculated from catch statistics and the estimated size of the spawning stock.

Dominion Bureau of Statistics records show that 6.6 million pounds (2994 metric tons) of herring were landed in Gloucester County, N.B., during April, May and June, 1962. For statistical purposes Gloucester County is divided into 4 districts (Fig. 1) and in District 65 where the spawning survey was made landings amounted to 2.2 million pounds (998 metric tons). Counts of quantities of herring gave an average value of 338 fish per 100 pounds (745 fish per 100 kg) and hence the number of herring landed in District 65 was 7.4×10^6. The size of the spawning stock was estimated at 185×10^6 fish (Table II).

On the above basis the rate of exploitation was

$$\frac{7.4 \times 10^6}{185 \times 10^6} \times 100 = 4\%$$

However, there were at least three spawnings in District 65 that were not included in the survey. These were reported by fishermen to be located near Caraquet, Caraquet Island and on Pokesudie Shoal (Fig. 1). Commercial catches in these areas were of the same order of magnitude as catches at Blanchard Point. Hence, an exploitation rate of 4% is excessive and the correct value probably lies nearer to 1 than to 4%.

Predation

Predation on the herring spawning bed at Blanchard Point must have been substantial. Winter flounders (*Pseudopleuronectes americanus*) could be seen everywhere and were extremely abundant in areas of medium and heavy egg deposition (Fig. 7). Maximum abundance of flounders was estimated at 1 per square foot (11 per sq m) in areas of heavy egg deposition and average abundance for the part of the bed surveyed by Scuba divers was estimated at 1 per square yard (over 1 per sq m). The distended abdomens of these flounders was ample evidence of their feeding activity. A few were caught and their stomachs examined. They contained nothing but herring eggs. The stomachs of three flounders 23, 31 and 38 cm (total length) contained 4980, 12,936 and 16,582 herring eggs, respectively. It is interesting to speculate that in a single meal for the total flounder population on the surveyed area the consumption of herring eggs may have been 5 billion or more. This represents approximately 0.14% of the estimated total number of eggs on the spawning bed. Assuming that 50 days would elapse from the beginning of spawning to the end of hatching, the egg mortality due to flounders was probably not less than 7% and may have been much higher.

In addition to the winter flounders there were large numbers of sculpins (*Myoxocephalus* sp.), skate (*Raja* sp.), smelt (*Osmerus mordax*) and lumpfish (*Cyclopterus lumpus*) on the spawning bed. One specimen of each species was examined and all except lumpfish were feeding on herring eggs.

The mortality of eggs on the spawning bed was apparently due almost entirely to fish predators. The number of dead or unfertilized eggs in the samples appeared negligible on examination and no estimate was made. The birds in the area (chiefly gulls) were feeding on herring and smelt, and except

FIG. 7. Underwater photograph of "heavy" egg deposition and predators (winter flounders).

in the most shallow areas they were probably unable to reach the eggs. There were no storms (at least none prior to May 24) that might have dislodged the eggs and cast them up on the beaches as sometimes happens in the Gulf of St. Lawrence.

Production and Distribution of Larvae

One of the interesting aspects of the survey was the visual evidence of hatching. On the afternoon of May 24 there were several patches of cloudy water near the southwest end of the spawning bed. Plankton tows in the area showed that the cloudiness was due to large numbers of newly-hatched herring larvae. In one 10-minute tow from a row boat near the herring trap (Fig. 3) 772 larvae (5–7 mm long and with yolk sacs still attached) were captured. This tow was made with a 1-m plankton net (12–15 meshes per inch or 5–6 meshes per cm) and the towing speed was less than 0.5 knots (0.9 km per hour). In four other tows made in a northeast direction away from the spawning bed using the same net but towing from the M. V. *Harengus* at about 2 knots (3.6 km per hour), the catches of larvae were 394 and 33 in the first two tows, respectively, and none in the last two.

The fact that no larvae beyond the yolk-sac stage were captured indicates that hatching had only just started. The patchy distribution of larvae indicates waves of hatching similar to those observed for spawning and which were often 3 or 4 days apart.

Too few plankton tows were taken to indicate the area distribution of larvae but they were probably being swept northeastward away from the spawning bed and out of Chaleur Bay in the general direction of the ebb-tide flow and the non-tidal surface drift.

SUMMARY

A survey of a herring spawning bed was carried out in May 1962 near Blanchard Point on the south side of Chaleur Bay, N.B. The principal technique for the survey was free-diving although a Petersen grab was used at the beginning and near the end of the survey.

The outside (seaward) edge of the spawning bed was mapped by divers who swam along this edge and either released marker buoys or surfaced and indicated where they should be released. The shape and dimensions of the bed were plotted later by taking compass bearings between each marker buoy and establishing their distance apart with a range finder.

Sampling was accomplished by establishing a series of transects across the long axis of the spawning bed and using a form of "cookie cutter" made from 6-inch (15-cm) stovepipe, to standardize samples. Thus each sample was from approximately 28.5 square inches (183.9 sq cm) of sea bed.

The spawning area surveyed by divers measured approximately 880 × 260 yards (805 × 238 m) and that sampled by the Petersen grab 1100 × 200 yards (1000 × 180 m) for a total area of 448,800 square yards (375,200 sq m).

Herring eggs were attached to seaweeds and varied in density from 1.18 to 17.54 million per square yard (1.5 to 21.9 million per sq m). The density of eggs was directly related to the density of vegetation or the presence of fishing gear. It was quite noticeable that there were fewer eggs where the alga cover was sparse and there were no eggs at all on bare gravel, sand or rocks. In the deeper areas of the spawning bed the vegetation consisted mainly of species of *Phyllophora* and *Laminaria* with occasional patches of *Furcellaria*. In the shallower areas it was mainly *Chondrus*, *Fucus* and *Ascophyllum* with small areas of *Zostera*.

Very few dead or unfertilized eggs were observed but there were large numbers of predators (chiefly winter flounders). Stomachs of the flounders contained from 4980 to 16,582 herring eggs each.

The total number of eggs on the spawning bed was estimated to be 35.46×10^{11} and the number of spawners 185×10^{6} fish. Using this estimate of total spawning stock size and the commercial catch in the immediate vicinity the fishing mortality rate was calculated to be 4%.

Hatching of herring eggs started about May 24 about 3 weeks after the beginning of spawning. Concentrations of newly-hatched larvae (5–7 mm long) could be observed visually and large numbers were taken with plankton nets.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the help of Captain H. H. Butler and the crew of the M. V. *Harengus* whose active interest and co-operation contributed immeasurably to the success of the work. We also wish to express our gratitude to Mr C. A. Dickson who assisted in carrying out the field program and to Mr C. F. Monaghan who with Mr Dickson undertook the tedious and exacting assignment of counting eggs in the laboratory.

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NOTES

A Sea Water Aquarium for Marine Animal Experiments

Experimental work with live fish and shellfish requires the maintenance of large numbers of animals in surroundings compatible with their continued good physiological condition. This note briefly describes the facilities and sea water supply recently installed at this laboratory for the purpose of holding and working with live marine animals under conditions approximating the natural environment. A more complete description and discussion is provided in a circular (Stewart and Power, 1963) which can be obtained from this laboratory.

Sea water is piped from a point in Halifax harbour 600 ft from shore and 50 ft below the surface of the water at low tide[1]. The pipeline terminates in a concrete lined pit sunk in one end of the aquarium building where the pipe is attached to two priming and screening boxes. A centrifugal, cast-iron pump (alternating with a standby) is run continuously to pump the sea water from one of these boxes. Water from the pump is filtered first through sand and gravel (coarse filtration), passed through a small-pore size filter (fine filtration or polishing), then led into an overhead piping system to be distributed to the animal holding tanks in the aquarium.

The aquarium consists of a structural steel framework supporting two levels of insulated fibreglass tanks, each level containing 21 tanks. Sea water is fed from overhead piping through a valve installed on the lead to each tank to control the inflow. A standpipe set into the corner of each tank provides drainage and water level control. All tanks drain into a common pipe which leads to the city sewage system. The upper level of tanks is darkened and is exposed to automatically varied illumination (Stewart, 1963).

In general, ferrous metals, in contrast to many other metals, are not toxic to marine animals; however, every effort has been made to use non-metallic materials. In the few places where it was found necessary to use metal, cast iron or Type 316 stainless steel was used.

A schematic diagram (Fig. 1) shows the general layout and major features of the running sea water system. The seaward terminus of the water intake is a screen-topped plastic-lined concrete bracket or anchor. The end of the pipe is cast permanently in the concrete. The water pipe which extends from the anchor to the building was custom-made in one piece. The extreme underwater length of the pipe (600 ft) was made necessary by inshore contamination of the water. The height of the bracket (8½ ft) ensures that the end of the pipe is kept well off the muddy bottom.

Annular 30 lb weights made of concrete cast around 8-inch lengths of 4-inch black polyethylene pipe through which the water pipe was threaded, hold the pipeline in position on the harbour bottom.

Laying operations were completed in approximately 5 hours. A floating crane took the concrete anchor aboard leaving the spool of pipe on the wharf,

[1]In Canada, the Department of Public Works and the National Harbours Board have jurisdiction over navigable waters and harbours, respectively. Permission must be sought from and granted by these agencies before any "works" can be placed in waters under their control.

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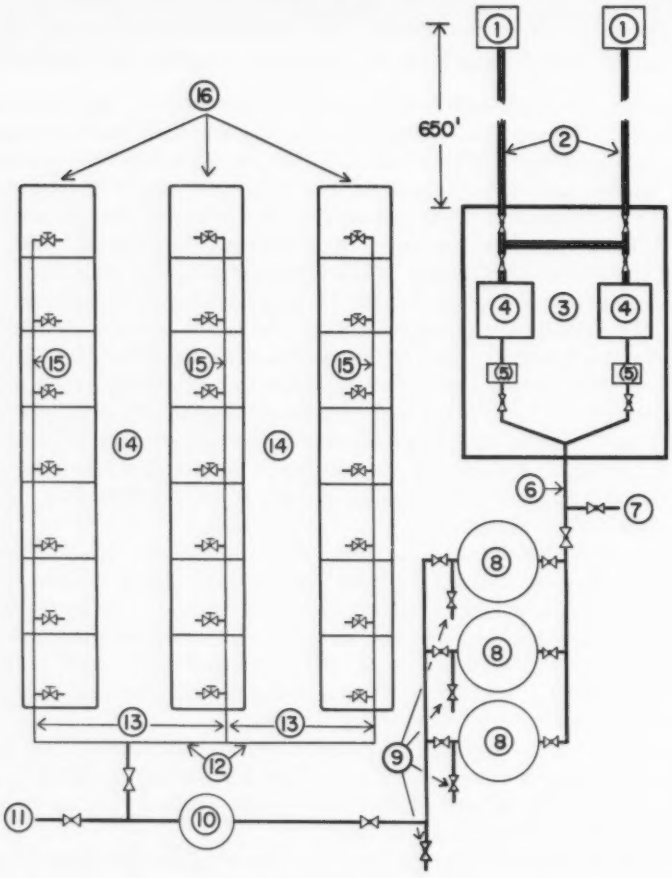

FIG. 1. Schematic diagram showing the general layout and major features of the aquarium and sea water supply system: (1) concrete water intake brackets and anchors; (2) 3 inch polyethylene pipelines; one pipeline is in place and the other will be laid soon; (3) concrete lined pit; (4) priming and screening boxes; (5) pumps; (6) 1½ inch rubber pipe; (7) bypass or water-outlet valve; (8) sand and gravel filters; (9) water outlets to drains; (10) sparkler filter; (11) bypass or additional water outlet; (12) 1 inch plastic pipe; (13) ¾ inch plastic pipe; (14) raised walk way; (15) ½ inch plastic pipe; (16) upper storey of animal holding tanks; the dimensions of each tank are 3 ft × 3 ft × 18 inches deep.

then kedged slowly backwards to the predetermined site, thereby stringing the pipe on the water surface. The weights were slid on, spaced at 12-ft intervals, tied in position, and the concrete anchor lowered. The pipe sank gradually as the air was replaced by water. All of the work was completed on the surface since the pipe floated until the air was expelled, even after the addition of the weights.

Fouling of the pipeline by materials large enough to block the water intake is prevented by the screen attached to the top of the concrete anchor. Materials which collect or cling to this screen may be removed by reversing the direction of water flow or, in exceptionally difficult cases, by a diver.

The large quantities of suspended materials found in these waters is removed by updraft sand and gravel filters (Fig. 2). Filters of this design work efficiently at a service flow rate equal to or less than 3 Imperial gallons per minute (IGPM) per sq ft of surface area. Increasing the rate of flow to 9 IGPM per sq ft of

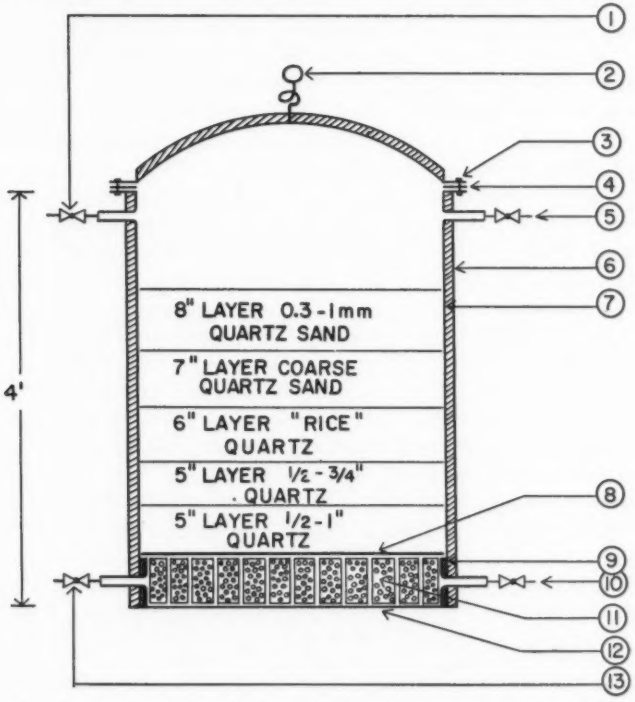

FIG. 2. Sand and gravel filter: (1) 1½ inch polyvinyl chloride (PVC) ball valve water outlet; (2) pressure gauge; (3) flanges coupled with brass nuts and bolts; (4) rubber gasket; (5) 1½ inch PVC ball valve water outlet; (6) 2 inch thick insulation with waterproof facing; (7) strongly reinforced fibreglass wall; (8) removable, $\frac{5}{16}$ inch thick, fibreglass shelf with ¼ inch perforations; (9) fibreglass support for outer edge of removable shelf; (10) 1½ inch PVC ball valve water inlet; (11) 5 inch lengths of 3 inch diameter, Class B, polyethylene pipe with ⅜ inch perforations; (12) strongly reinforced, fibreglass bottom; (13) 1½ inch PVC ball valve additional water inlet or drain.

surface area for 5 to 10 min washes the filter satisfactorily by lifting and tumbling the sand in the higher velocity water. After the wash water appears to be clean the flow is reduced to service rates and the water passing through the filter is run out the drain for 10 min. Washing and resettling of the sand beds is now

complete and the filter is returned to service. The frequency of washing, which depends upon the amount of suspended solids in the water, is easily determined during the early stages of operation. The size of the individual filter unit is generally limited by the amount of water available for washing a single unit. Fresh water, of course, can be used to supplement the sea water for washing purposes.

The authors intend to polish the water by passing the effluent from the sand and gravel filters through a Sparkler Tube Filter[2,3] which has 8 perforated tubes lined with high wet-strength paper, providing approximately 20 sq ft of filtration surface. The rated capacity of this type of filter is 3 IGPM per sq ft of surface area. Without prior filtering through sand and gravel, all polishing procedures fail because of the rapid clogging of the filter media.

Air supply lines strung overhead inject air into the water in each tank through an "air stone". An air supply is necessary when the animals' requirements exceed the amounts of oxygen naturally dissolved in the water such as occurs in temporary overloading of the tank or through failure of the pumps.

Approximately 1 IGPM is required to keep the 60 Imperial gallons in each insulated tank within 1 C° of the temperature of the incoming water when a 20 C° differential exists between the room and incoming water temperatures.

The facilities described above are extremely versatile and can be used for keeping a wide variety of marine animals. Very little work is needed to convert part or all of the system to a fresh water supply or to a closed, recirculating system. At present, the list of animals held in running sea water taken from Halifax harbour include salmon, cod, lobsters and oysters. Part of the system is supplied with dechlorinated fresh water and is being used to hold young salmon, trout, and salmon eggs for experimental work.

The cooperation and help of the Naval Research Establishment, Defence Research Board, Dartmouth, Nova Scotia, Mr L. E. Baker, Maritime Area Director, Department of Fisheries of Canada, and the National Harbours Board is gratefully acknowledged. Special thanks are due Mr J. Cuddy, Maintenance Supervisor, Naval Research Establishment, Dartmouth, Nova Scotia for his extremely useful advice and supervision of the pipeline installation.

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[2]Sparkler International Ltd., Toronto, Ontario.

[3]Mention of a manufacturer's product is made for the purpose of providing a more exact description and is not to be taken as an endorsement of these products by the Fisheries Research Board of Canada.

Common Porpoise from the Stomach of a Greenland Shark

A young specimen of the common porpoise, *Phocoena phocoena* (L.), was found in the stomach of a 4.15 m (13 ft 6 inches) long female Greenland shark, *Somniosus microcephalus*, captured on June 11, 1962 on the northeastern slope of the Grand Bank of Newfoundland. The record is noteworthy in furnishing data on the distribution of the common porpoise and on the season and size of birth in this remote part of the range.

The shark was caught in Lat. 46°32′45″N, Long. 47°22′30″W in the otter trawl of the Fisheries Research Board's *A. T. Cameron* which was fishing in 326 m (178 fath). Surface temperatures varied between 1.3 and 3.2° C during the 9-day period the vessel was fishing near this position. No sightings of living porpoises were noted in the ship's log despite good weather and visibility.

The porpoise was 79 cm (2 ft 7 inches) long, weighed 7.70 kg (17 lb) and was in very good condition except for the eyes which had been somewhat digested. In the blubber on the top of the head were a few sharp cuts which had presumably been made by the shark's teeth. The stomach was completely empty of either solid matter or milk. Raw edges of tissue around the unhealed umbilicus marked where the umbilical cord must have separated off recently. All the teeth still lay beneath the gums. The porpoise calf was evidently still-born or only a few hours old when it died.

Further information relating to the breeding of common porpoises in the northwest Atlantic is provided by Dr H. D. Fisher who, from his studies of these animals in the Bay of Fundy, has kindly supplied the following records for publication.

Specimen	*Length*	*Date*	*Notes*
Female foetus	70 cm	June 20, 1953	
Female foetus	84 cm	May 24, 1954	largest foetus
Female calf	90 cm	Aug. 13, 1949	smallest calf
Female calf	95 cm	Aug. 15, 1949	milk in stomach
4 lactating adult females		taken between July 11 and mid September	

On the European side of the North Atlantic the size at birth of the common porpoise is in the 60–80-cm range (Fraser, 1953; Dudok van Heel, 1962).

Sergeant and Fisher (1957) report that common porpoises are to be seen in Newfoundland and Labrador coastal waters from May to October. The centres of their summer distribution in the northwest Atlantic, however, are in the Bay of Fundy and around the Magdalen Islands (D. E. Sergeant, personal communication, July, 1962). The wintering area does not appear to be known.

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I am grateful to Mr A. W. May, the scientist in charge of the cruise of the *A. T. Cameron*, for the original data on which this note is based and to Drs H. D. Fisher and D. E. Sergeant of the Fisheries Research Board of Canada Arctic Unit for helpful advice and information.

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On the Demersal Quality of the Fertilized Eggs of Pacific Cod, *Gadus macrocephalus* Tilesius

For many years it was assumed, presumably on the basis of observations on Atlantic cod, that the eggs of the Pacific cod are pelagic. Moiseev (1953) refers to the work of Marakava who in 1918 believed that eggs of cod from the western coast of Kamchatka were pelagic and to the work of Rass and Zheltankova who in 1948 believed that cod eggs exhibited a demersal quality only in the laboratory.

Uchida (1936) is one of the first to state that the cod egg in the Pacific is truly benthic. Yamamoto and Nishioka (1952) state that eggs are truly demersal and that they are slightly adhesive. Their determinations on the specific gravity of the fertilized cod egg yielded a value of 1.052. Tamura (1952) suggests that some cod eggs are buoyant if they are larger than 1.35 mm in diameter. Moiseev (1953) states that the cod egg has no oil globule, is slightly adhesive, and sinks to the ocean floor. Rass (1959) reversed his earlier conclusions and states that the Pacific cod has demersal adhesive eggs.

The foregoing observations apply to waters of the northwestern Pacific Ocean. Heretofore, there has been no comparable information on cod of the northeastern Pacific.

In 1961 and 1962, the author made two tests of the buoyancy of cod eggs in British Columbia waters. The first was conducted on a cod spawning ground in northern Hecate Strait. Eggs from a ripe female were extruded into a bucket and mixed with milt from a ripe male cod. Samples of the eggs were then placed in clear plastic tubes (60 cm in length; 5 cm in diameter) which had been filled with artificial sea-water of various salinities. The eggs were observed to sink even in water with a specific gravity of 1.0266 (salinity of 34‰ at 7.5° C). Although the actual specific gravity of the eggs was not determined, it was concluded that the eggs must tend to sink to the bottom because the specific gravity of the sea water overlying the cod spawning ground rarely exceeds 1.0265.

The second test was made on cod taken from a spawning ground in the Strait of Georgia (Nanoose Bay). Eggs and milt were taken from a pair of ripe cod and mixed in a bucket. Sub-samples of fertilized eggs were placed in the plastic tubes and a concentrated solution of salts added until the eggs no longer sank. The solution in which most of the eggs had a neutral buoyancy was then analyzed in the laboratory and the specific gravity calculated. The calculations showed that the eggs had a specific gravity of 1.050, close to the result obtained by Yamamoto and Nishioka (1952). Proof that the eggs were viable and fertilized was demonstrated by laboratory hatching of other sub-samples.

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Thanks are due to Mr K. V. C. Stephens for the preparation of the artificial sea water and the analysis of the solutions.

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Measurements of Immature Stages of *Triaenophorus*

As part of the biological investigation of *Triaenophorus crassus* Forel carried out at Heming Lake, Manitoba, several series of measurements of eggs, coracidia and procercoids from this lake and from other regions were made. Measurements were made on living material with a Whipple eyepiece grid which had been calibrated against a stage micrometer. The purpose of the work was to determine whether there were any obvious morphological differences between *Triaenophorus* parasites from widely separated geographic regions. Measurements of eggs and coracidia reported by Ekbaum (1937) and Miller (1943, 1952) were available for comparison. Detailed descriptions of eggs, coracidia and procercoids have been reported by Miller (1952) and Watson and Lawler (1961).

Representative samples of eggs of both *T. crassus* and *T. nodulosus* (Pallas) were measured and the details of the size and range in length and width are given in Table I. The size of eggs of both species appeared highly similar. Although

TABLE I. Comparison of *T. crassus* and *T. nodulosus* eggs from several sources.

	Lake				
	Heming 1953	Heming 1957	Huron 1958	Nipissing[a]	Lesser Slave[b]
		T. crassus			
Sample size	53	7	101	...	...
Average length μ	57.1	57.6	58.1	58	61
Average width μ	36.6	37.4	37.9	40	41
Range of length μ	48–65	55–61	47–66	54–64	53–68
Range of width μ	31–43	36–38	32–43	36–44	38–44
		T. nodulosus			
Sample size	18	56	...	...	...
Average length μ	56.9	56.2	...	...	61
Average width μ	38.4	37.7	...	...	41
Range of length μ	47–66	50–62	...	...	58–67
Range of width μ	34–43	34–46	...	...	38–44

[a]From Ekbaum, 1937.
[b]From Miller, 1943.

the values obtained by Miller (1943) from the Lesser Slave Lake material are slightly higher for both *T. crassus* and *T. nodulosus*, it would appear that there are no distinct differences in the average size and range of size of eggs of either species between the widely separated areas under comparison.

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The average length and width of coracidia of both *T. crassus* and *T. nodulosus* are shown in Table II. Coracidia of both species are approximately of the same proportions and there do not appear to be any significant differences between coracidia of either species from different localities. The junior author, after a reasonably thorough examination, was unable to distinguish species by distinctive characters of the coracidial hooklets.

TABLE II. Comparison of *T. crassus* and *T. nodulosus* coracidia from several sources.

	Lake			
	Heming 1953	Huron 1958	Nipissing[a]	Lesser Slave[b]
		T. crassus		
Sample Size	50	12	...	...
Average length μ	...	57.6	...	73
Average width μ	...	53.3	...	54
Range of length μ	59–84	50–67	60–70	67–80
Range of width μ	46–65	46–67	50–60	58–80
		T. nodulosus		
Sample size	43	...	...	...
Average length μ	...	...	...	75
Average width μ	...	...	...	68
Range of length μ	43–92	...	...	67–85
Range of width μ	44–84	...	...	58–80

[a]From Ekbaum, 1937.
[b]From Miller, 1943.

Eggs and coracidia of *T. crassus* and *T. nodulosus* were introduced to plankton samples from Heming Lake. It was found that the North American subspecies, *Cyclops bicuspidatus thomasi*, readily became infected with both species of *Triaenophorus*. No difficulty was experienced in maintaining *C. bicuspidatus* in the laboratory, and so it was possible to follow the growth and development of both *T. crassus* and *T. nodulosus* from the coracidium to the mature procercoid in the body of the plankton host. The number of copepods in the various cultures ranged from 2 to 12 and the number of procercoids in individual copepods from 1 to 5. The growth and development of procercoids of both species is shown in Fig. 1. These data represent the average size of all procercoids in the respective samples and do not indicate the range in size or the individual differences in size between animals. It is seen that the growth is relatively slow and that the ultimate size attained is considerably less than that shown by Miller (1943) for procercoids of the same species. For example, at Heming Lake the average size of a procercoid of *T. crassus* after 8 days was 73 μ, while Miller (1943) found

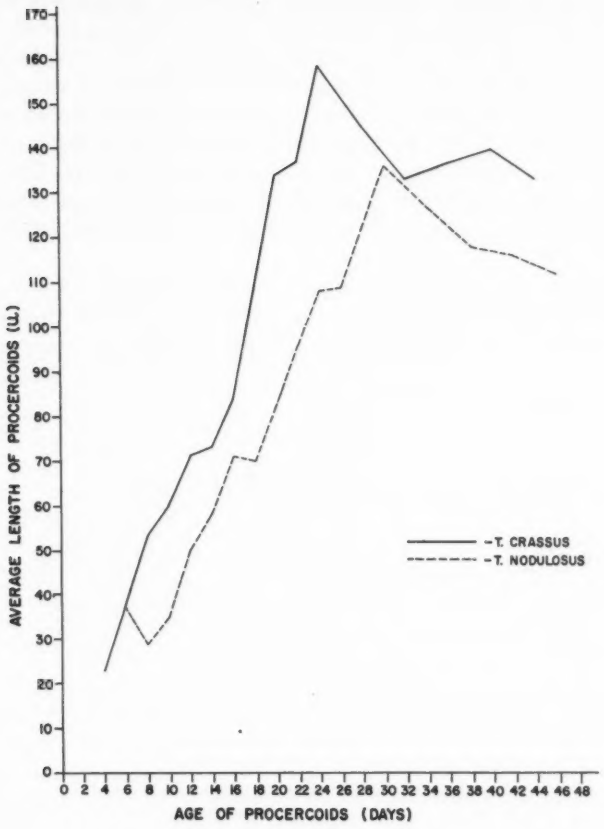

FIG. 1. Growth of procercoids of *T. crassus* and *T. nodulosus* in *Cyclops bicuspidatus* infected experimentally at Heming Lake, Manitoba.

procercoids as large as 300 μ. The present investigation has shown that the number of parasites per host has some effect on their growth rate; the growth rate of procercoids in heavily infected copepods is retarded and the ultimate size attained is not as large as in the lightly infected copepods. This factor, however, does not explain the obvious size difference between Heming Lake and Lesser Slave Lake experimental procercoids. Consideration was given to the effect of temperature on the rate of development, and it is believed that this factor was responsible for the retarded growth observed in the Heming Lake experiment. The cultures were kept in very cold ground where the temperature remained fairly constant at 39 to 40° F (3.9 to 4.4° C) for over a month. Only when the cultures were examined every second day were they subjected to higher or

fluctuating temperatures. By the end of July the temperature in the cooler did reach 58° F (14.4° C). In contrast to this, Miller (1943) carried out this experiment when the room temperature varied from 55 to 70° F (12.7 to 21.1° C). Libin (unpublished manuscript)[1] showed that the growth of the procercoids in *C. bicuspidatus* and *C. strenuus* was considerably accelerated in cultures held at 56 to 60° F (13.3 to 15.5° C), compared to those held at 42 to 50° F (5.5 to 10° C). This difference in developmental temperature coupled with the fact that it has already been shown that the constant cold temperature retarded the development of the eggs and coracidia probably accounts for the diminutive size of the Heming Lake procercoids.

The growth of a procercoid (possibly, but not distinguishable as, *Triaenophorus*) from a *Cyclops* infected in nature was compared to the growth of procercoids in experimental infections (Fig. 2). The size of the procercoid in the

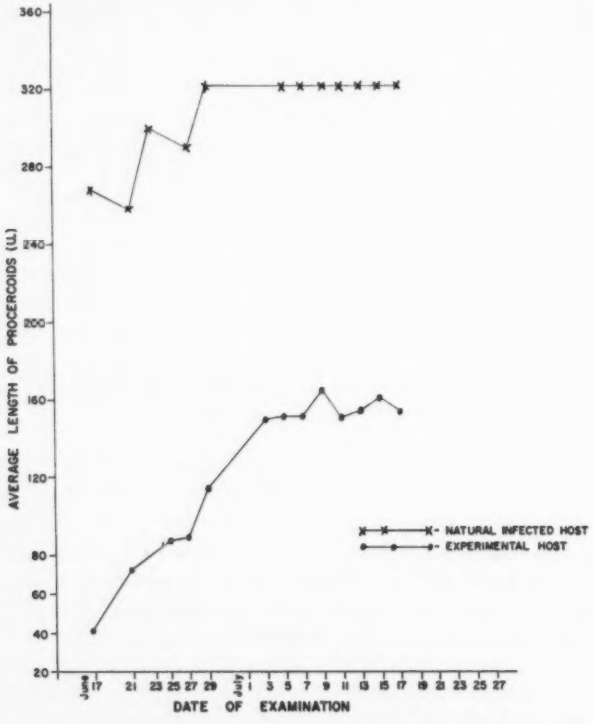

FIG. 2. Comparison of the growth of procercoids in a naturally infected host and an experimentally infected host at Heming Lake, Manitoba.

[1]Appendix 15 to Central Fisheries Research Station mimeographed Annual Report for 1953 available at all Board stations.

naturally-infected copepod increased for about 10 days and levelled off at what was probably the maximum size. Although the procercoids continued to live in the experimental host's body cavity until the death of the latter a month later, they failed to attain the size of the one from the natural infection.

The cercomere or caudal appendage, according to Miller (1943), is an indication that the procercoid is mature and that after the cercomere is established, the procercoid within stops growing or grows very slowly. Cercomeres were observed in procercoids as small as 144 μ. The majority of procercoids which continued to grow slowly for such a long time before dying did not exhibit cercomeres.

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A Further Record of the Blacktail Snailfish, *Careproctus melanurus* Gilbert, from British Columbia Waters

On November 2, 1962, a specimen of the blacktail snailfish (*Careproctus melanurus* Gilbert) was caught by Mr O. J. Hansen, skipper of the trawler *Aleutian Queen*, while fishing in 133–160 fathoms off the west coast of Vancouver Island. Location of capture was the "Esteban Deep" which is approximately 27 miles SSW of Esteban Point (49°10′N, 127°W). Identification was made with the aid of a key prepared by Burke (1930).

Distribution of the species is from northern British Columbia to California. However, only two other specimens have been recorded from British Columbia waters (Clemens and Wilby, 1961, p. 350). The first of these was taken in 1888 between the northern end of Vancouver Island and the southern end of Moresby Island (Queen Charlotte Islands) by the *Albatross*, Station 2860, Lat. 51°23′N, Long. 130°34′W, depth 876 fathoms. The second specimen was caught in June 1953 in Swanson Channel, Strait of Georgia, by a trawler fishing in 49 fathoms.

On advice from Dr C. L. Hubbs (personal communication with W. E. Barraclough, March 12, 1954) some special features not covered in Clemens and Wilby's description should be mentioned. They are as follows: a very low insertion of the pectoral fin, the base of which is nearly horizontal; base of the upper rays of the pectoral hardly as high as the premaxillaries on median line of the snout; gill openings confined to region above pectoral base, but relatively wide owing to the low insertion of the fin; teeth slender, very small, without cusp, a little flattened on terminal portion and a little widened (halbert shaped) behind tip.

These special features appeared in unpublished notes (1916) of Dr C. H. Gilbert in reference to the type specimen USNM 44285 taken at *Albatross* Station 2925.

The low insertion and nearly horizontal base of the pectoral fin was apparent on the specimen from Esterban Deep (Fig. 1) as well as on the one from Swanson Channel.

The present specimen, 26.5 cm in total length, has been deposited in the museum of the Institute of Fisheries at the University of British Columbia (Cat. No. BC 62-641).

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FIG. 1. *Careproctus melanurus* Gilbert. Caught by trawler *Aleutian Queen* (O. J. Hansen, Skipper) while fishing in 133–160 fathoms at Esteban Deep on November 2, 1962. Total length 26.5 cm.

An Occurrence of Opah, *Lampris regius* (Bonnaterre), in the Northwest Atlantic

On September 10, 1962, an opah or moonfish (*Lampris regius*) was captured by the longliner *Sen Sen* (Captain Wesley Ross) while fishing for halibut on the "81" peak which is about 110 miles south (true) of Halifax, N.S. (approximate location Lat. 42°46′N, Long. 63°15′W). This fish was landed at Clark's Harbour, N.S., and shipped to Yarmouth where it was held until September 19. It was then transferred to the St. Andrews (N.B.) Station of the Fisheries Research Board of Canada where it was examined by the authors.

This specimen had the right eye and most of the mouth parts torn out in taking it off the trawl hook. Further damage included torn membranes between the anal fin rays and the lower posterior part of the dorsal fin. However, 9 days after capture it was still the most colourful fish we have ever seen. The head and body were a dark violet colour with a silvery cast and covered with silvery white spots. The spots were round to oval in shape, varied in size (longest diameter) up to 17 mm and while numerous on the dorsal and upper lateral surfaces were doubly so on the ventral parts of the body. The skin was thin and easily torn revealing the "salmon"-pink flesh beneath. The ventral surface from the mouth to the insertion of the pelvic fins had a distinct rosy shade superimposed on the other colouration. The fins and the remaining pieces of the jaws were scarlet to vermillion with sparsely scattered silvery white spots which were quite distinct except on the dorsal surface of the pectorals. In general, the body colouration of our specimen was more like the colour plate of LaGorce (1952) than that of Clemens and Wilby (1961) although the fin colour was closer to the latter than the former.

The fork length of our specimen was 113 cm, the greatest body depth 66 cm and the weight 49 kg. The depth of the caudal peduncle was 7.1 cm. The greatest height of the dorsal fin was 24.3 cm; the pectorals 31.4 cm; the ventrals 26.3 cm and the first ray of the anal 7.0 cm. Both the dorsal and ventral fins were falcate; the former with 52 rays and the latter with 17 rays. The pectorals were slender and conspicuously pointed with 21 rays. The anal fin extended from the vent to the caudal peduncle, varied little in height and had 39 rays. The caudal fin was strong and distinctly forked. The scales were small and irregularly shaped. Other conspicuous features were the large eye (7.9% of fork length), the strongly arched lateral line, the horizontal insertion of the pectoral fins, and the distinct dorsal and ventral pre-caudal pits.

Orkin (1950) found 50 beaks of the oceanic squid in a single opah stomach. The stomach of our specimen contained one small octopus and the remains of 25 small fish, 10 to 15 cm long, which were probably argentines (*Argentina silus*).

The opah is usually considered to be pelagic, an inhabitant of the open oceans, both Atlantic and Pacific (Herald, 1939). Presumably it lives mainly in deep water, for Orkin (1950) in assembling records of its occurrence stated that it was

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often taken off the coast of Europe in 100 fathoms near the edge of the Continental Shelf. However, when taken at the surface or in shallow water it is apparently as a solitary individual. Farran (1923) describes its behaviour near the surface as aimless and confused, quite evidently being out of its accustomed habitat.

Off the Pacific coast of North America, Herald (1939) reported "Twenty-four opahs are known from California waters; however it is possible that some of these records may be duplicates . . . there are five specimens in addition to the 24 from California". Clemens and Wilby (1961) reported that the first specimen was taken in British Columbia waters on August 25, 1935, with numbers of others since.

In the eastern Atlantic it is "rare but widely distributed (off southern Africa) mostly in deep water, only twice found near the Cape" (Smith, 1950). It is rarely found in the Mediterranean. Its range is from Madeira northward to Iceland and Finland. Numerous specimens have been caught around the British Isles and Jenkins (1925) reported that almost one a week was taken during September in the waters west of the Shetlands.

In the western North Atlantic its range seems to be northward from and including the coast of Maine though it has been taken near Cuba (Breder, 1929) and off the west coast of Florida (Gudger, 1926). On the whole it is a straggler on the eastern coast of North America, and in fact almost everywhere, as all records refer to individual captures of this species.

There are 9 recorded captures of opah in the northwest Atlantic including the present one. Jordan (1889) recorded the capture of a 60-inch (152-cm) specimen on the Grand Banks in 1888 and states "the opah was once before recorded from the Newfoundland Banks". Jones (1882) reported a capture near Sable Island in 1856 but gave no details. Shufeldt (1893) reported a capture on LaHave ridges with no date or other details. Harper (1928) recorded the capture of a 31¼-inch (79-cm), 32-pound (14.5-kg) opah near Hyannis, Cape Cod on September 17, 1928. Vladykov (1935) recorded the capture of a 54.8-inch (139-cm) specimen on Browns Bank in the spring of 1932. Bigelow and Schroeder (1953) reported a 165-pound (75-kg) opah taken on Georges Bank in August 1947.

The paucity of recorded captures in the northwest Atlantic emphasizes the scarcity of this species in this region and though it is found somewhat more frequently in the northeast Atlantic it seems doubtful that it can be looked upon as a future food resource as suggested by Herald (1961).

The authors are pleased to acknowledge the assistance of Mr W. Murdock, Manager of British Columbia Packers Limited at Clark's Harbour, N.S. Mr Murdock realized that this was an unusual specimen and arranged for its delivery to Mr E. G. Sollows at the Yarmouth office of the Fisheries Research Board of Canada.

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An Occurrence of Dusky Sharks, *Carcharhinus obscurus*, (Lesueur) 1818, in the Northwest Atlantic

On September 23, 1962, four dusky sharks (*Carcharhinus obscurus*) were caught from the Fisheries Research Board of Canada's research vessel *A. T. Cameron* in the Corsair Canyon region of Georges Bank. They were part of a school of 8 or 10 sharks presumably all of the same species which appeared around the vessel while a bottom trawl catch was being sorted. The catch which consisted chiefly of haddock, *Melanogrammus aeglefinus* (Linnaeus), argentine, *Argentina silus* Ascanius, silver hake, *Merluccius bilinearis* (Mitchill) and squid, *Illex illecebrosus* (Lesueur), was being discarded and the sharks were feeding on the discards. The sharks were caught by handlines with #13 Mustad tuna hooks using whole squid as bait. Fishing took place at the surface at Lat. 41°20′00″N, Long. 66°10′30″W. Surface temperature and surface salinity were 19.3°C and 34.57‰, respectively.

The four specimens caught were all males, 310, 329, 314 and 317 cm total length and weighed 177, 200, 209 and 191 kg, respectively. Identifying characters included: (a) the dirty gray colour, (b) the broadly rounded and flat snout, (c) the dermal ridge between the 1st and 2nd dorsal fins, (d) the free part of the 2nd dorsal less than twice its vertical height, (e) a vertical line from the origin of the 1st dorsal falling behind the pectoral, (f) the eye diameter less than the length of the 5th gill opening and (g) the absence of white tips on the fins. Proportional dimensions in percent.of total length are listed below. All measurements except fin margins were made as straight lines between points.

Fork length: 82.4, 79.5, 79.2, 79.4

Snout length in front of: Nostrils 5.7, 4.2, 5.3, 4.8; eye 8.2, 6.9, 8.5, 8.0; mouth 6.8, 6.2, 6.7, 6.4

Snout to origin of: Pectoral 23.0, 22.4, 23.8, 24.2; first dorsal 34.0, 30.9, 33.1, 32.5; anal 66.8, 63.3, 65.7, 66.1; caudal 75.4, 72.6, 74.3, 72.9

First dorsal fin: Vertical height 9.6, 7.9, 8.7, 6.9; base length 8.6, 8.9, 8.5, 8.4

Anal fin: Vertical height 3.1, 2.6, 3.4, 3.2; base length (attached) 3.7, 3.8, 4.2, 4.0; base length (to end free tip) 6.9, 6.9, 7.1, 6.6

Caudal fin: Upper margin 26.1, 27.0, 25.5, 26.1; lower margin 12.3, 12.4, 12.9, 12.0; peduncle width 3.0, 3.2, 3.5, 2.9; peduncle depth 3.4, 3.1, 3.3, 3.4

Body at origin of pectoral: Breadth 13.1, 12.5, 13.7, 13.0; depth 12.7, 12.7, 12.9, 13.2

Interspace between: First and second dorsals 23.8, 24.5, 25.7, 23.2; second dorsal and caudal 6.7, 6.8, 6.7, 6.4; anal and caudal 5.3, 5.8, 5.5, 5.4

Pectoral fin: Length anterior margin 19.8, 20.1, 22.0, 19.6

Nostrils: Distance between inner ends 6.5, 5.8, 6.0, 6.4

Eye: Horizontal diameter 1.0, 1.0, 1.0, 1.0

Mouth: Width 10.0, 9.3, 10.5, 9.2

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The dusky shark is common in the waters off the coast of Florida and Louisiana (Bigelow and Schroeder, 1948) but has not been reported from the western Gulf of Mexico or along the Atlantic coast between Florida and Delaware Bay. It has been positively identified from Delaware Bay north to Woods Hole, Massachusetts, from which area have also come a number of unconfirmed reports. To the north and east of Woods Hole there are, according to Bigelow and Schroeder (1948), only two reliable records of the occurrence of dusky sharks; one from Nantucket shoals and the other from Georges Bank. The Georges Bank record was originally reported by Firth (1931) who wrote "One specimen 11 feet long was captured August 10, 1931, on the northeast peak of Georges Bank . . . this species has heretofor not been recorded in the offshore waters of the Gulf of Maine". The four captures in September 1962 thus add to the very meagre knowledge of dusky shark distribution in offshore areas of the northwest Atlantic.

The lower jaws of three of these dusky shark specimens are preserved and stored (catalogue No. 22,113) at the Royal Ontario Museum, Toronto, Ontario. The complete head of the fourth specimen is preserved and stored (Accession No. 62–209) in the National Museum of Canada, Ottawa, Ontario.

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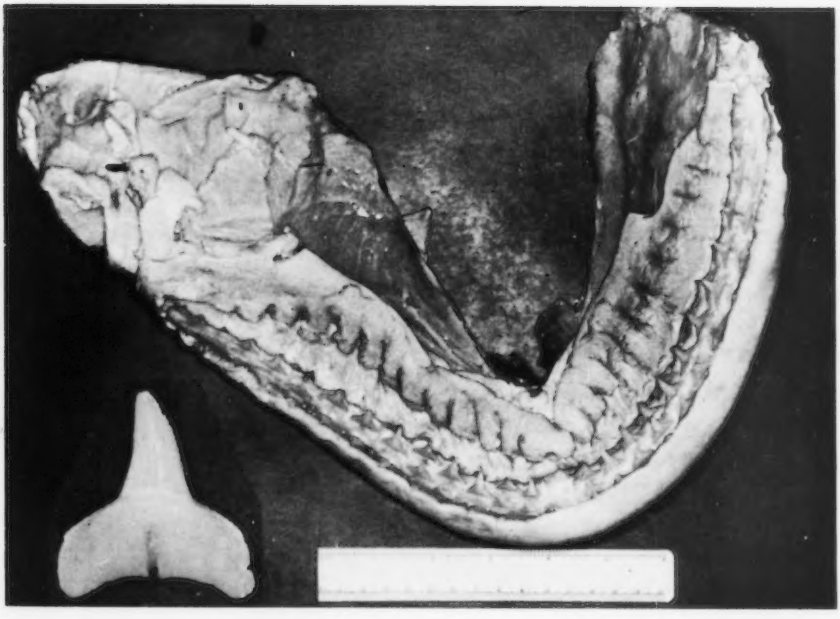

FIG. 1. Lower jaw of dusky shark, *Carcharhinus obscurus*, with single tooth shown in inset (photo by P. W. G. McMullon).

An Arrangement for Automatically and Reproducibly Controlling and Varying Illumination in Biological Experiments

Light is a variable under natural conditions and has been implicated as a factor in biological phenomena ranging from planktonic blooms to the behaviour of birds. Consequently any study or manipulation of biological systems, particularly those involving the whole animal, should include a consideration of illumination. Edmondson (1956) and Strickland (1958) ably demonstrated the biological importance of illumination in their discussions of aquatic photosynthetic productivity.

This note describes a versatile and inexpensive arrangement for illuminating an extensive system of tanks, cages or other enclosures allowing the amount of light to be varied continuously and reproducibly throughout a 24-hr cycle. Repetition of the 24-hr program is automatic and the system requires no attention other than periodic inspections and the time necessary for making the appropriate program changes. Control is achieved through voltage changes in the power fed to the operating unit, thus the controls are quite easily adapted for use on any arrangement or instrument whose performance can be varied by voltage changes. The lighting system used in this laboratory illuminates 21 square tanks, each 3 feet wide, with one 10-watt, frosted, incandescent light bulb and wide bay reflector centrally positioned 3 feet from the water surface of each tank. Extraneous light is excluded from the bank of tanks by black polyethylene sheeting.

Incandescent bulbs have been used since their output can be varied by voltage changes and they closely approach the relative spectral distribution of daylight radiation in the visible and near ultraviolet range. Radiation above the visible end of the spectrum may be ignored if the lighting conditions are intended to duplicate those existing at a depth greater than 2 m (Clarke, 1939); in fact, penetration of water by radiation above 10,000 *A* is limited to the first 10 cm. Data on the amount of solar radiation reaching the earth's surface, its modification by the atmosphere, and its penetration of waters may be obtained from the reviews of Edmondson (1956) and Strickland (1958) or from the original sources listed by these authors.

A schematic diagram of the physical layout (Fig. 1), a wiring diagram (Fig. 2), a picture of the control unit (Fig. 3), and a parts list are included as an aid to construction. The exact location of the control unit parts, as shown in Fig. 1, is not critical but care should be exercised to obtain good mechanical advantages.

Variation in the illumination of the tanks is achieved by increasing or decreasing the voltage of the electrical current fed to the lights. Control of the voltage is maintained through a Powerstat variable transformer which in turn

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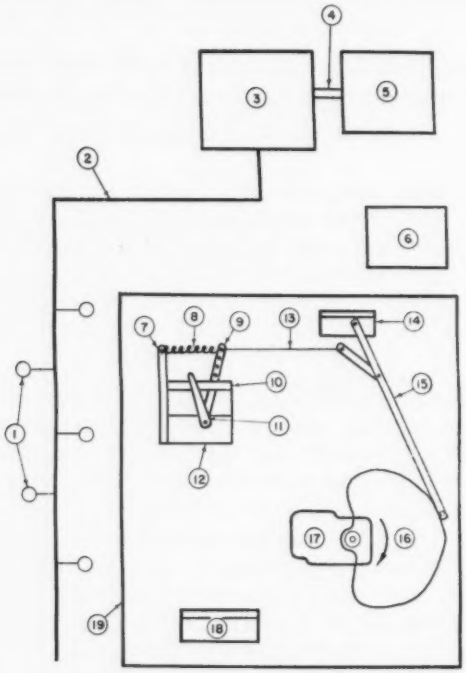

FIG. 1. Schematic diagram of the physical layout of the lighting system: (1) lights, (2) electrical load line, (3) Powerstat variable transformer, (4) fibre drive shaft, (5) Modutrol motor, (6) 24-volt transformer; (7) through (12), taken collectively, represent the proportioning resistor: (7) aluminum bracket, (8) soft wire spring, (9) aluminum arm, (10) 140-ohm resistor, (11) slide arm, (12) gear mechanism, (13) non-stretching drafting cable, (14) small block of wood — axle mount of cam follower arm, (15) cam follower arm, (16) lucite cam, (17) chart drive mechanism, (18) heater-resistor, (19) type E wiring cabinet.

is operated by a control system whose point of origin is the 24-hr chart drive mechanism as shown in the diagrams. A $\frac{1}{8}$-inch thick lucite cam of appropriate shape attached to the chart drive mechanism completes one 360° revolution every 24 hr. The channeled wheel on the cam follower arm rides on the cam and traces its perimeter; the other end of the arm rotates on an axle mounted on a small block of wood bringing the arm into the plane of the cam. Tension is maintained on the cam follower arm through a length of non-stretching, drafting cable attached to an aluminum arm which is fastened to the main shaft of the proportioning resistor or potentiometer gear mechanism. This arm is held

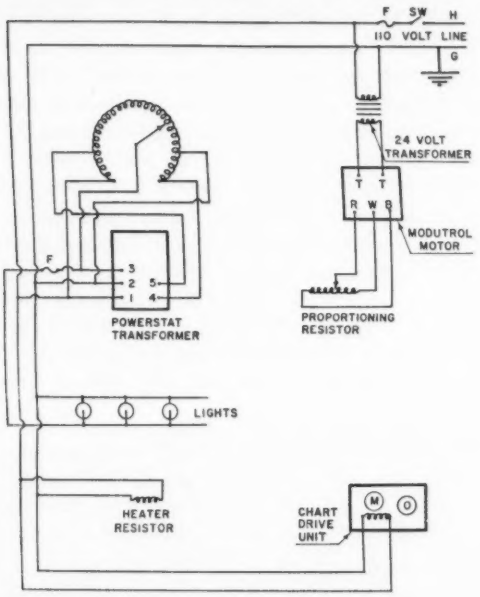

Fig. 2. Wiring diagram of the lighting system.

taut by a spring incorporated in this gear mechanism and by a soft wire spring anchored to an aluminum bracket. The aluminum arm and bracket are not integral parts of the potentiometer and must be made and attached after purchase of the unit. Rotation of any cam except a circular model results in related changes in the slide arm of the proportioning resistor and a corresponding unbalancing of the Wheatstone bridge circuit formed between the proportioning resistor and the matched potentiometer in the 240° drive Modutrol motor. Current then flows, starting the Modutrol motor which moves to a new position rectifying the imbalance in the bridge circuit. The motor movement, via a fibre drive shaft, changes the setting of the Powerstat variable transformer to a new position thereby increasing or decreasing the voltage of the current to the lights. A 24-volt transformer feeds electrical current to the bridge circuit and the Modutrol motor. The majority of the controls are mounted on a firm base of ½-inch marine plywood which is fastened by wing nuts to the back of a Type E wiring cabinet. Thus the panel can be removed conveniently for maintenance or alteration by detaching several wires and removing the wing nuts. A 1500-ohm, 50-watt resistor has been installed in the cabinet as a heater to keep dampness and resultant damage to a minimum.

Since variations in voltage are not proportional to changes in light intensity the unit must be calibrated in terms of some illumination unit such as foot candles or watts per degree or unit of change in the position of the cam follower arm. The easiest and most accurate method of calibration is to select and install a

light bulb whose range in intensity meets the illumination requirements and then by means of a calibration cam and light meter obtain the settings on the cam follower arm for the complete range of illumination. The settings of the cam follower arm corresponding to the desired illumination values in foot candles or other units can then be marked at the required times on a 24-hr recording chart (circular, 12-inch). A line connecting these points forms the outline of the suitable cam. This outline is traced on and cut from $\frac{1}{8}$-inch lucite. The leading edges of the cam must present less than a perpendicular traverse to the cam follower arm or the cam will lock on the arm and prevent the chart drive mechanism from turning. A durable calibration cam can be made from a 12-inch circular plate of $\frac{1}{8}$-inch lucite with a series of small holes drilled at $\frac{1}{4}$- or $\frac{1}{2}$-inch intervals along the line of the arc described by the end of the cam follower arm in a path from the centre of the mounted circular lucite plate to the outer edge. Small pegs inserted in the holes will hold the cam follower arm in position while the light readings are taken.

The variable transformer in this system will operate up to a maximum output of approximately 825 watts on a 110-volt line, but can be replaced with a heavier unit with no other change if the load is to be increased beyond this level. The 240° drive Modutrol motor allows a range of approximately 90 volts with the transformer used; if the full 110 volts are required a motor with a larger drive arc should be substituted.

Parts List[1]

(1) Type E Wiring Cabinet (18″ wide × 20″ high × 5″ deep)
Amalgamated Electric Co., Montreal, Quebec.

(2) Heater-Resistor — 1500-ohm, 50-watt
Ohmite Manufacturing Co., Chicago, Illinois.

(3) Twenty-four Hour Chart Drive Mechanism (Part No. 74105 — Chart Drive Motor; Part No. 74063 — Gear Train)
Honeywell Controls Ltd., Toronto, Ontario.

(4) Cams — $\frac{1}{8}$ inch thick lucite.

(5) Cam Follower Arm (Part No. 361789)
Honeywell Controls Ltd., Toronto, Ontario.

(6) Non-Stretching Drafting Cable; Metal Braid Cable for Parallel Ruling Attachment (Cat. No. 0212700)
Hughes Owens Co. Ltd., Halifax, Nova Scotia.

(7) Modutrol Motor 240° Drive Arc. 24-volt, 17-watt (Part No. M 904E1119)
Honeywell Controls Ltd., Toronto, Ontario

(8) Powerstat Variable Transformer (Model No. 116,0–140 volts, 7.5 amps)
Superior Electric Co., Bristol, Connecticut

(9) Proportioning Resistor — 140 ohm (Part No. 352030–2 — Resistor; Part No. 351995 — Gear Mechanism)
Honeywell Controls Ltd., Toronto, Ontario

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[1]Mention of a manufacturer's product is made for the purpose of providing a more exact description and is not to be taken as an endorsement of these products by the Fisheries Research Board of Canada.

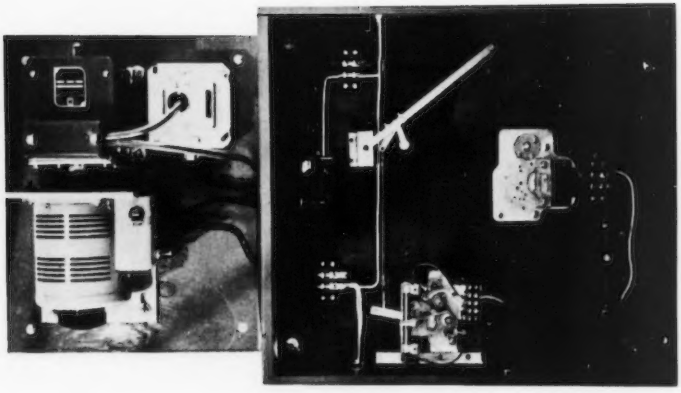

Fig. 3. Photograph of the lighting system's control unit.

(10) Transformer 25 volts, 40 volt/amps. (Part No. AT 72D1048)
Honeywell Controls Ltd., Toronto, Ontario

(11) Thermoplastic Wire, Type T.W. — Low Voltage 16 ga.; High Voltage 14 ga.

(12) Fibre Drive Shaft, Custom machined, insulating fibre rod reinforced with a brass shell

(13) Soft wire spring, aluminum arms and brackets, and electrical plugs are all of standard manufacture and are generally available.

The author thanks Mr J. W. Gates of this Laboratory, and Mr B. R. Roberts of Honeywell Controls Limited, for the technical assistance and advice which made the lighting system's operation successful. In addition the author expresses his appreciation for the photographic work done by Dr J. R. Dingle.

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Report for the fiscal year ended March 31, 1962. (1962, 205 pp., 75 cents.)

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